AN IN-DEPTH INVESTIGATION OF RESOURCE FISHES WITHIN AND SURROUNDING A COMMUNITY-BASED SUBSISTENCE FISHING AREA AT HĀʻENA, KAUAʻI

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ABSTRACT

Nearshore fisheries in Hawai‘i have been steadily decreasing for over a century. Marine Protected Areas (MPAs) have been proposed as a method to both conserve biodiversity and enhance fisheries. I compared biomass and abundance of fisheries resource species inside and outside a recently established MPA on the north shore of the island of Kaua‘i. The Hā‘ena Community Based Subsistence Fishing Area (CBSFA) employs a unique adaptive management strategy from which rules and regulations were established in 2015. *In situ* visual surveys of fishes, invertebrates, and benthos were conducted using a stratified random sampling design to evaluate the efficacy of the MPA, beginning in 2016. L_{50} values—defined as the size at which half of the individuals in a population have reached reproductive maturity—were used as proxies for identifying reproductively mature resource fishes both inside and outside the CBSFA. Surveys between 2016 and 2018 revealed significantly higher resource fish biomass outside the CBSFA boundaries, at deeper sites both within and outside the boundaries, as well as in pavement habitats compared with other habitat types. Although several species had higher biomass and abundances within the CBSFA boundaries, there was no strong evidence for a reserve effect at this time.

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CHAPTER 1. INTRODUCTION

Overfishing is one of several proximate drivers that directly affect the health of coral reef ecosystems worldwide (Cinner and Kittinger 2015). Overfishing has major environmental and socioeconomic impacts that have reduced marine biodiversity and modified ecosystem functions on both global and local scales (Pinsky et al. 2011; Worm and Branch 2012). Commercial catch records have identified a decline in Hawai‘i’s nearshore fisheries over the last century due to intensified fishing pressures, land-based pollution, habitat destruction, and the introduction of invasive species (Friedlander et al. 2014). Although subsistence and recreational fishers tend to catch many species with a variety of fishing gear, the catch is often unreported and undocumented, making the non-commercial nearshore fishery difficult to manage (McCoy et al. 2018).

Contemporary, western-style Marine Protected Areas (MPAs) have recently been gaining acceptance as a method of conserving and enhancing nearshore fisheries (Gaines et al. 2010; Friedlander et al. 2019). MPAs can benefit fisheries areas surrounding the MPA through reproductive output, as well as by providing adult spillover (Gaines et al. 2010; Burgess et al. 2014). The effectiveness of MPAs is dependent on aspects such as size, shape, location, configuration, larval recruitment, life-history traits, habitat types, and levels of community and stakeholder involvement (Agardy 2000; Gaines et al. 2010; Burgess et al. 2014; Lubchenco and Grorud-Colvert 2015).

In the State of Hawai‘i, approximately 17% of nearshore waters have some level of protection but only 3.4% of nearshore waters are highly protected (Friedlander et al. 2019). Existing MPAs in Hawai‘i range in size with a median area of 1.2 km^2, and encompass a variety of protection, enforcement, and effectiveness levels (Friedlander et al. 2019). MPAs with high

protection levels support greater resource fish biomass and MPAs in remote locations support a healthy fish trophic structure in relation to MPAs near high human populations; habitats with high variation and complexity provide the most effective MPAs (Friedlander et al. 2019).

The Kahekili Herbivore Fisheries Management Area (KHFMA) on the island of Maui is an example of an MPA with restrictions on herbivorous species but is otherwise open to other fishing activities (Williams et al. 2016). Increased biomass and abundance of herbivorous species were apparent within six years of the establishment of the KHFMA. The Pūpūkea Marine Life Conservation District supported higher biomass after size expansion and increased enforcement (Friedlander et al. 2019). The Waikīkī-Diamond Head Shoreline Fisheries Management Area is an example of rotational fishing restrictions employed in alternating years and has been demonstrated to be ineffective at increasing fish biomass, abundance, and diversity (Williams et al. 2006).

In 2006, a type of MPA called a Community-Based Subsistence Fishing Area (CBSFA) was established in Hā‘ena, Kaua‘i. Rules and regulations for the CBSFA were established in 2015 through the collaboration of the Hā‘ena community and the state of Hawai‘i. The following year, the Hawai‘i Department of Land and Natural Resources (DLNR), through the Division of Aquatic Resources (DAR), and the Division of Boating and Ocean Recreation (DOBOR), partnered with the Hawai‘i Institute of Marine Biology (HIMB), Coral Reef Ecology Lab (CREL), and the Coral Reef Assessment and Monitoring Program (CRAMP) to conduct surveys within and directly outside the recently established Hā‘ena CBSFA to determine the efficacy of recently enacted regulations. This collaborative research effort included rapid assessment surveys of fish species number and size and benthic coverage both inside and outside the CBSFA. Annual monitoring is proposed to continue for a five-year period followed by a re-

evaluation of the efficacy of the CBSFA. Adaptive environmental assessment and management will be used throughout this time through meetings with DAR and community members as an integrative process to further manage objectives and accrue information required to improve the future management structure of the area.

Although the five-year survey period is not yet complete, the Hā‘ena community has requested information on resource fishes surveyed between 2016 and 2018. Resource fishes are species that are targeted by humans for consumption. The Hā‘ena community created a list of important resource species that are caught for subsistence and are, therefore, the species they wish to protect (Appendix 1 and Appendix 2). Additional species, not on the Hā‘ena community's species list, were added in this study. Species added include several invasive species, as well as other resource species that are often targeted by fishers statewide (Appendix 1).

The following study focuses on resource fish assemblage structures and their habitat affinities within the CBSFA following the 2015 management regime implementation. Several measures of reproductive maturity were used to examine temporal changes in abundance and biomass of reproductively mature individual resource fishes inside and outside the CBSFA over a three-year period.

1.1 Research questions and objectives

Question 1: Is resource fish biomass changing by year (2016, 2017, 2018) and by location (inside vs. outside the CBSFA)?

Question 2: Is the estimated abundance of reproductively mature resource fishes increasing by year (2016, 2017, 2018) and by location (inside vs. outside the CBSFA)?

Question 3: How do habitat types affect resource fish biomass within and outside the Hā‘ena CBSFA?

CHAPTER 2. BACKGROUND

2.1 Nearshore coral reef fishes

Although fishes make up only a portion of a diverse tropical coral reef ecosystem, they fill numerous niches and are overall a functionally diverse group (Barneche et al. 2014). Fish assemblages are composed of a variety of feeding guilds including detritivores, herbivores, omnivores, and piscivores, all of which contribute to the complex coral reef ecosystem as nutrient cyclers and trophic level controllers (Barneche et al. 2014; Mouillot et al. 2014). Within such a diverse group of organisms with varying functional roles and demands for energy (Barneche et al. 2014), it is necessary for some species of fishes to travel longer distances than others to fulfill their energy, reproductive, and social requirements (DeMartini et al. 2011; Green et al. 2015; Weeks et al. 2016). How well MPAs function in rebuilding nearshore fisheries depends on several factors: adult and juvenile movement (Botsford et al. 2009), larval dispersal, and habitat preferences (Gaines et al. 2010; Speed Rossiter and Levine 2013; Green et al. 2015).

Fishes that spend most of their time inside MPA boundaries are theoretically safe from fishers, yet it is understood that there is increased likelihood that more mobile fishes will venture outside the boundaries depending on their life stage, food availability, and reproductive state (Meyer et al. 2000; Howard et al. 2009; Eble et al. 2009; Gaines et al. 2010; Schemmel et al. 2016). The ideal free distribution hypothesis explains how individuals of a species may distribute themselves based on the resources that are available to them (Abernethy et al. 2007). Individuals will likely settle in areas where the acquisition of fitness benefits is maximized. As this ideal habitat acquires individuals, the benefits of this habitat will begin to decrease as shelter and food availability decreases. Eventually, the fitness benefits for individuals will decrease to the point where they reach similar levels to habitats that may have fewer benefits. Therefore, an expansion

of the ideal free distribution hypothesis is that habitats where fitness benefits are maximized will be settled first and the densities of individuals in the lower quality habitats will be fewer than those in the higher quality habitats. One of the assumptions for the ideal free distribution hypothesis is that the behavior of these individuals is constant, although this is often not the case in the natural world (Abernethy et al. 2007).

Because individuals of the same species tend to migrate to and remain in habitats that provide more benefits than neighboring habitats, designing MPAs to incorporate higher quality habitat would be ideal. Habitat quality is dependent on each species' requirements for shelter, food availability, etc. (Berglund et al. 2012; Stevenson et al. 2013). In choosing a larger area with a lower quality habitat versus a smaller area with higher quality, the smaller area may be more beneficial, as more individuals would be suited to occupy the higher quality area. However, the quality of a small area is density dependent. As the density of individuals begins to increase, neighboring areas would also become inhabited due to the spillover effect. Larger MPAs with higher quality habitat (i.e. higher diversity and complexity) will provide greater benefits to exploited species (Pittman et al. 2009; Berglund et al. 2012; Graham and Nash 2013; Wedding et al. 2019). Therefore, increasing abundances and biomass of fishes within the CBSFA will depend on what the fishes of the area perceive and require as optimal habitat.

2.1.1 Life-history stages and ontogenetic shifts

Depending on their life stage, fishes prefer different habitat types and shift their locations to accommodate their needs. These ontogenetic shifts mean that fishes may change their range of movements several times during their life cycle, depending on diurnal effects, seasonal effects, and food availability (Botsford et al. 2009).

For some species, planktonic larval stages may last several days to several months before settling back on a reef (Hamilton 2008). Even as juveniles, local and seasonal shifts may occur depending on thermal tolerances, food availability, shelter, and salinity (Hamilton 2008; Llopiz and Cowen 2009; Grorud-Colvert and Sponaugle 2011; Peck et al. 2012). Eventually, juveniles will make habitat shifts that are more suitable for their adult phases (Appeldoorn et al. 2003; Jones et al. 2010). As adults, they may prefer deeper water where they can forage for food. During this stage, individuals will also likely shift their location and habitat preferences in relation to location or spawning seasons. When these individuals are ready to spawn, another major shift in habitat may occur, such as moving to deeper water where ocean currents can provide food and/or carry larvae away from predators near the reef.

Friedlander et al. (2007) found that in Hawai‘i, areas with larger depth ranges were correlated with a higher biomass of fishes, as opposed to nearshore habitats with narrower depth ranges. The diversity of fishes may also be higher in deeper habitats (Friedlander et al. 2003). Throughout their life cycles, fishes in the Hawaiian Archipelago migrate perpendicular to shore where depth range is greater and habitat variability is, therefore, higher, allowing a greater number of species to exist (Friedlander et al. 2007). The placement of MPAs should, therefore, account for nearshore and offshore habitats that are beneficial to resource fish life cycles.

2.1.2 Fish habitat associations

Incorporating quality habitats for all life stages of fish species within MPA boundaries has been shown to result in higher abundances and biomass of exploited species (Friedlander et al. 2007b; Jones et al. 2010; Berglund et al. 2012; Friedlander et al. 2019). In Hawai‘i, *Scarus rubroviolaceus* and *Caranx melampygus* are examples of culturally significant, often heavily exploited, nearshore coral reef fish that vary in life-history traits (Sudekum et al. 1991;

DeMartini et al. 2018). *S. rubroviolaceus* is site-attached, yet individuals have been known to migrate away from home ranges for reproductive reasons, sleeping site locations, and sex-changes that occur within the species. This species has been found in habitat types with high coral cover and high rugosity (Howard et al. 2008; DeMartini and Howard 2016). In contrast, *C. melampygus*, a top-level predator, is a highly mobile species with wide home ranges (Sudekum et al. 1991). It tends to occupy the entire water column but remains connected to demersal habitats in shallow waters (Sudekum et al. 1991).

Although studies have shown that Hawai‘i fish biomass tends to be higher in habitats that provide more shelter from wave exposure (Friedlander et al. 2003) and habitats with higher complexity (Wedding et al. 2019; Chung et al. 2019), predatory species such as *C. melampygus* have been associated with high wave energy zones and sand channels (Friedlander et al. 2003; Friedlander et al. 2007b). Friedlander et al. (2007b) found that apex predators in the Main Hawaiian Islands (MHI) utilize sand channels as corridors between hard bottom habitats, highlighting the importance of these habitats for ecosystem function and the need to include sand channels when deciding where to place and extend MPA boundaries. Incorporating an interconnected network of MPAs by utilizing some of these protected “runways” composed of sandy habitats may aid species such as *C. melampygus* as they move and migrate between MPAs (Friedlander et al. 2003).

2.2 Reproductive maturity of resource fishes

The combination of reduced fishing pressure and the availability of favorable environments allows fishes within an MPA to increase their reproductive output (Kaiser et al. 2007; Schemmel and Friedlander 2017). In 1938, von Bertalanffy created a growth model that

incorporates body size as a function of age that has become the basis for assessing fish populations and stocks (Fig. 1; von Bertalanffy 1957). The von Bertalanffy model has been used to show how stochasticity affects the probability of fish growth rates (von Bertalanffy 1957; Lv and Pitchford 2007). Because growth affects fecundity (Hixon et al. 2014), reproductive potential can also be derived.

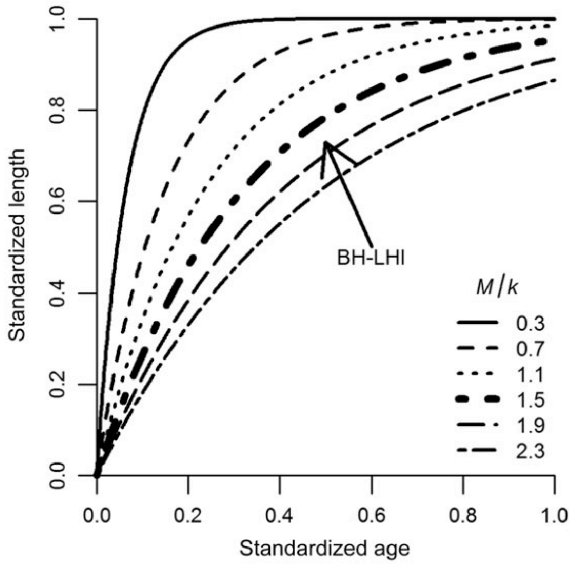

Figure 1. Example of a von Bertalanffy growth curve applied to life-history parameters referenced from Hordyk et al. (2014). M/k refers to the ratio of natural mortality over growth rate of the individual, and BH-LHI refers to Beverton-Holt life history invariants. BH-LHI are proxies for values of ratios, such as M/k, that predict life history parameters in data poor stocks.

A recent study found that larger females produce disproportionately more abundant and quality eggs than smaller females to the point at which decreases in fish size due to overharvesting and warming waters will severely affect the ability for populations to replenish (Barneche et al. 2018). Big Old Fat Fecund Female Fish (BOFFFF) has been shown to increase the reproductive potential of fisheries and greatly increase the productivity of stocks (Hixon et al. 2014; Barneche et al. 2018). The larger the female fish, the more likely it is to produce abundant, quality eggs. BOFFFF larvae have been found to grow faster and survive their vulnerable stages

better than larvae from smaller female fishes (Hixon et al. 2014). Fishers usually target and overexploit BOFFFFs that would otherwise supply the next generation of individuals, ultimately selecting for populations with smaller sized individuals (Hixon et al. 2014). Although there are efforts to minimize fisheries exploitation, it takes time for fish populations to recover and reach a state of stability (Botsford et al. 2009; Worm and Branch 2012).

2.2.1 Parameters for assessing reproductive maturity

There are often factors in an environment that make it difficult to use mathematical models that do not involve stochasticity, as natural environments are constantly changing (Lv and Pitchford 2007). Although growth curves can be used to estimate several life-history parameters, it is difficult to understand spawning and fecundity without studying fish species *in situ* to develop the life history parameters that are required by mathematical predictions (Schemmel and Friedlander 2017). Several life history parameters can be derived from directly measuring the reproductive organs of many individuals, as well as recording lengths, weights, and ages of fishes (Schemmel and Friedlander 2017). Unfortunately, life history data at a species level is often lacking, as acquiring them is an intense process, and where present, there are wide ranges of variability in these traits globally, regionally, and locally (Sudekum et al. 1991; Longenecker and Langston 2008b; DeMartini and Howard 2016; Schemmel and Friedlander 2017; DeMartini et al. 2018).

Stock assessments of large-scale commercial fisheries are typically based on mathematical modeling of life-history parameters using fisheries dependent data and are fairly accurate for the large sample sizes of catch that occur for global fisheries (Nadon et al. 2015). Nearshore fisheries are often data-poor, due to a wide diversity of species catch and limited management that can make accurate mathematical modeling challenging (Friedlander et al. 2014;

Nadon and Ault 2016). Nadon (2017) recently developed a stock assessment report for several of Hawai‘i’s nearshore coral reef fishes using maturity values, or L_{50} values that indicate the size at which half of the individuals within a population mature. This specific value is often derived from several known parameters, such as life span, mortality rates, growth rates, etc. (von Bertalanffy 1957; Hordyk et al. 2015; Nadon and Ault 2016).

L_{50} values can also be derived by individual gonad measurements in a population. However, L_{50} values can vary by location from which the values were derived, or from where the parameters for the mathematical functions were derived (Schemmel and Friedlander 2017). Schemmel and Friedlander (2017) have recently found that L_{50} values can vary between islands in Hawai‘i. This is because reproductive maturity for any given individual in a population varies by temperature, season, and fishing pressure (Fromentin and Fonteneau 2001; Kaiser et al. 2007). The use of L_{50} values as a parameter for assessing reproductive maturity will be discussed further in Chapter 3.

2.3 Adaptive management strategies

CBSFAs place local and traditional knowledge and practices at the forefront of fisheries management, allowing accountability for fisheries by local community members (Friedlander et al. 2018). One of the social side effects of most MPAs in Hawai‘i is the prevention of local fishers from practicing traditional fishing methods or incorporating adaptive management strategies due to temporary or permanent closures (Jokiel et al. 2011). The integration of local and traditional knowledge and practices into the CBSFA design gives local people who use the protected area on a frequent basis accountability and a voice that can be beneficial in creating rules and regulations, especially as there are many communities that still depend on marine

resources for subsistence. Contemporary research and management practices serve the purpose of providing the data that allows local stakeholders and communities to adjust their rules and regulations as needed, thus allowing an adaptive management strategy to take effect (Tissot et al. 2009). The Hā‘ena CBSFA may serve as a central model in the future development of other CBSFAs around the state.

2.3.1 Local traditional and customary knowledge

The Hawaiian people fished for subsistence long before western colonization. Their catch was strictly monitored by the *konohiki*[1] to ensure fishers followed *kapu*[2] (Titcomb 1977; ‘Ī‘ī 1993; Poepoe et al. 2003; Kahā‘ulelio 2006;). The *konohiki* managed the harvest by allowing fishers to fish in specific areas during certain times or restricting catch of certain species of fishes with long lifespans or low fecundity in order to have as little impact on the coral reef ecosystem as possible (Kosaki 1954; Maly and Maly 2004). The breaking of *kapu* resulted in severe consequences, sometimes as extreme as death (Kuykendall 1938; Malo 1951). The combination of strict *kapu* and immense knowledge that the ancient *konohiki* acquired from keen observation allowed the Hawaiian people to fish for subsistence for hundreds of years without depleting their limited resources (Kosaki 1954; Poepoe et al. 2007).

One way in which Native Hawaiians of the past practiced careful observation of their natural environment was by using lunar phases to predict fish spawning and recruitment patterns (Poepoe et al. 2007; Jokiel et al. 2011; Friedlander et al. 2013). Native Hawaiians noticed that fishes spawned, aggregated, and fed at specific intervals and seasons during different phases of

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[1] *konohiki* = overseers
[2] *kapu* = rules

the moon (Titcomb 1972; Poepoe et al. 2007). They then used the moon calendar as a guide to understand and regulate fisheries (Fig. 2; Maly & Maly 2003; Jokiel et al. 2011; Popepoe et al. 2007). Fishing regulations and seasonality of fishing practices were dependent on the moon calendar, so as not to disrupt the natural cycle of the fisheries (Poepoe et al. 2007). Several communities in Hawai‘i continue to use this strategy today to determine when and where they fish (Friedlander et al. 2013).

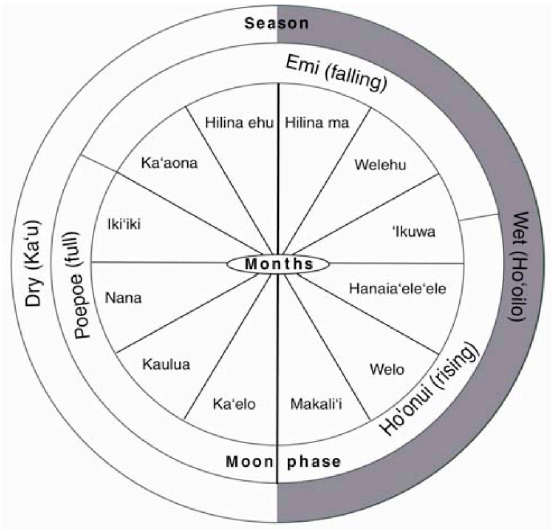

Figure 2. Moon calendar from the island of Moloka‘i that fishermen used for fishing (Poepoe et al. 2003).

2.3.2 Establishment history of the Hā‘ena CBSFA

In 1994, the Hawai‘i State Legislature passed a law to allow for the designation of CBSFAs in an attempt to encourage the co-management of marine resources, influence local fishers to develop appropriate fisheries harvest, and improve accountability for a locally sustainable and healthy marine coral reef ecosystem (Tissot et al. 2009). These types of MPAs were the first of their kind in contemporary Hawaiian natural resource management and are consistent with management practices prior to European contact. Although the CBSFAs in

Moʻomomi, Molokaʻi, and Miloliʻi, Hawaiʻi were created earlier, the Hāʻena CBSFA was the first legislative CBSFA to establish rules and regulations.

The establishment of the Hāʻena CBSFA began with the development of the Hui Makaʻāinana o Makana by the residents of Hāʻena in 1999 (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). In the 1900 census, 97% of the residents living in the Hāʻena community were native Hawaiians (Andrade 2008). By 2010, this percentage dropped to 22.7% due to natural disasters and the development of roads to the area (Andrade 2008). An increasing number of tourists and vacation rentals resulted in the breakdown of the traditional fisheries management system and an increase in anthropogenic influences that depleted the once-rich fisheries of Hāʻena (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources, 2016; Friedlander et al. 2018). The *kupuna*[3] of Hāʻena noted the decline in fishes linked to the loss of *konohiki*, recreational overuse, coastal development, and pollution (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). As descendants of Hāʻena experienced this generational shift, they created the Hui Makaʻāinana o Makana in hopes of restoring the *ahupuaʻa*[4]-based management system that facilitated the abundant historic fisheries of Hāʻena (Friedlander et al. 2013; Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016).

In 2006, the Hui Makaʻāinana o Makana and other community members petitioned the state and succeeded in designating the coastal reef at the base of the *ahupuaʻa* as a CBSFA (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). Over the next five years, community members and stakeholders of Hāʻena, community

[3] *kupuna* = elders
[4] *ahupuaʻa* = watershed

groups, including the Hui Maka‘āinana o Makana, and the State of Hawai‘i Department of Land and Natural Resources (DLNR) through the Division of Aquatic Resources (DAR) worked together to develop a management plan for the newly established CBSFA (Division of Aquatic Resources & Hawai‘i Department of Land and Natural Resources 2016). In 2011, the proposed management plan was submitted and accepted by DLNR (Division of Aquatic Resources & Hawai‘i Department of Land and Natural Resources 2016). The fishing rules and regulations for the CBSFA were then established in 2015 (Division of Aquatic Resources & Hawai‘i Department of Land and Natural Resources 2016).

2.4 Summary

MPAs are generally successful at conserving and enhancing fisheries when they are large and prevent fishing completely (Gaines et al. 2010; Friedlander et al. 2019). Additionally, MPAs must be self-sustaining by maintaining adequate larval recruitment (Gaines et al. 2010). If a MPA is too small, enhancement of fisheries within the boundaries will be dependent on fish larval recruits from heavily fished waters directly outside of MPA boundaries (Gaines et al. 2010; Burgess et al. 2014). A number of species with varying life-history traits are prominent within MPAs. Understanding whether a species of fish is fast or slow-growing, when and where it tends to aggregate and spawn, at what age and size it spawns, and how large it becomes, is critical for predicting the success or failure of a fishery as a whole (Hixon et al. 2014; Schemmel and Friedlander 2017). The process by which an individual becomes reproductively mature also varies by temperature, season, and other biotic or abiotic pressures (Fromentin and Fonteneau 2001; Kaiser et al. 2007).

In Hawaiʻi, studies have shown that *Caranx ignobilis* and *Caranx melampygus* are highly mobile piscivorous species that feed on crustaceans and cephalopods (Sudekum et al. 1991). *Parupeneus multifasciatus* are detritivores, broadcast spawners, and are less site-attached than species of Pomacentridae that tend to be small in size, site attached, and lay demersal eggs (Longenecker and Langston 2008a). Furthermore, coral reef fish assemblages can be heavily influenced by benthic structure depending on species' needs and ontogenetic shifts (Jones et al. 2010). Habitat types with high three-dimensional structure harbor greater biomass, abundance, and diversity of fishes, because complex structure provides shelter and refuge from predation (Graham and Nash 2013; Wedding et al. 2019). A network of MPAs that encompasses a variety of habitat types and incorporate larval and adult fish connectivity will provide the most successful protection of fisheries (Gaines et al. 2010; Berglund et al. 2012). With such a wide range of variability, adaptive management strategies may provide better opportunities to conserve an ever-changing nearshore ecosystem.

CHAPTER 3. METHODS

3.1 Biological surveys

3.1.1 Study site

This study was conducted at Hā‘ena, Kaua‘i in the state of Hawai‘i. Surveys were conducted within and outside the boundaries of the CBSFA (Rodgers et al. 2017; 2018; 2019). The boundaries of the CBSFA are located within the Hā‘ena *ahupua‘a* that is located in the larger Halele‘a *moku*[7] (Fig. 3). The CBSFA boundaries extend 1,610 m (1 mile) offshore and 5,633 m (3.5 miles) along the coastline and encompass sections of the Nā Pali State Park and Hā‘ena State Park.

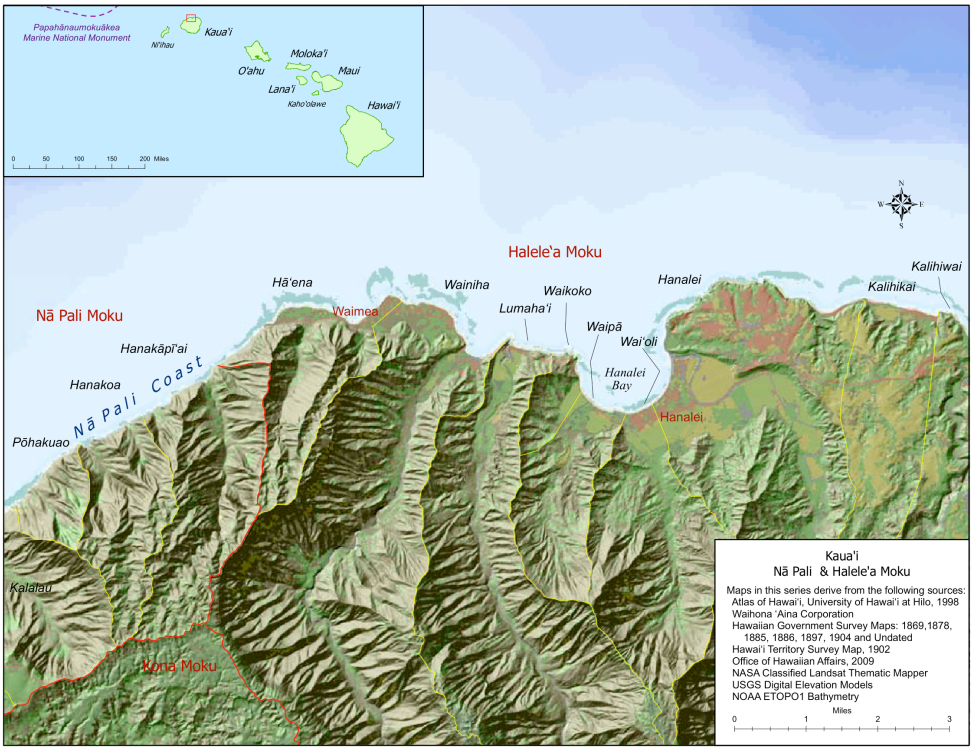

Figure 3. Halele‘a *moku* encompassing Ha‘ena and Hanalei (Glazier et al. 2012).

[7] *moku = region*

Within the CBSFA boundaries are several regulation zones with stricter fishing and vessel transiting rules including the ʻŌpihi Management Area, the Makua Puʻuhonua, and a Vessel Transit Boundary (Fig. 4; Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). The ʻŌpihi Management Area protects the limpets that grow on the rocky shores inside the CBSFA. Only 20 individuals may be harvested per person per day (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). The Makua Puʻuhonua is a small, shallow area on the backreef, inside the CBSFA boundaries, where fishing is prohibited. This area is meant to protect juvenile fishes that reside there (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). The Vessel Transit Boundary is designated to keep all vessels away from the shallow reefs and fishers that may be using those areas (Division of Aquatic Resources & Hawaiʻi Department of Land and Natural Resources 2016). Current fishing rules and regulations within the CBSFA pose restrictions on specific fishing gear.

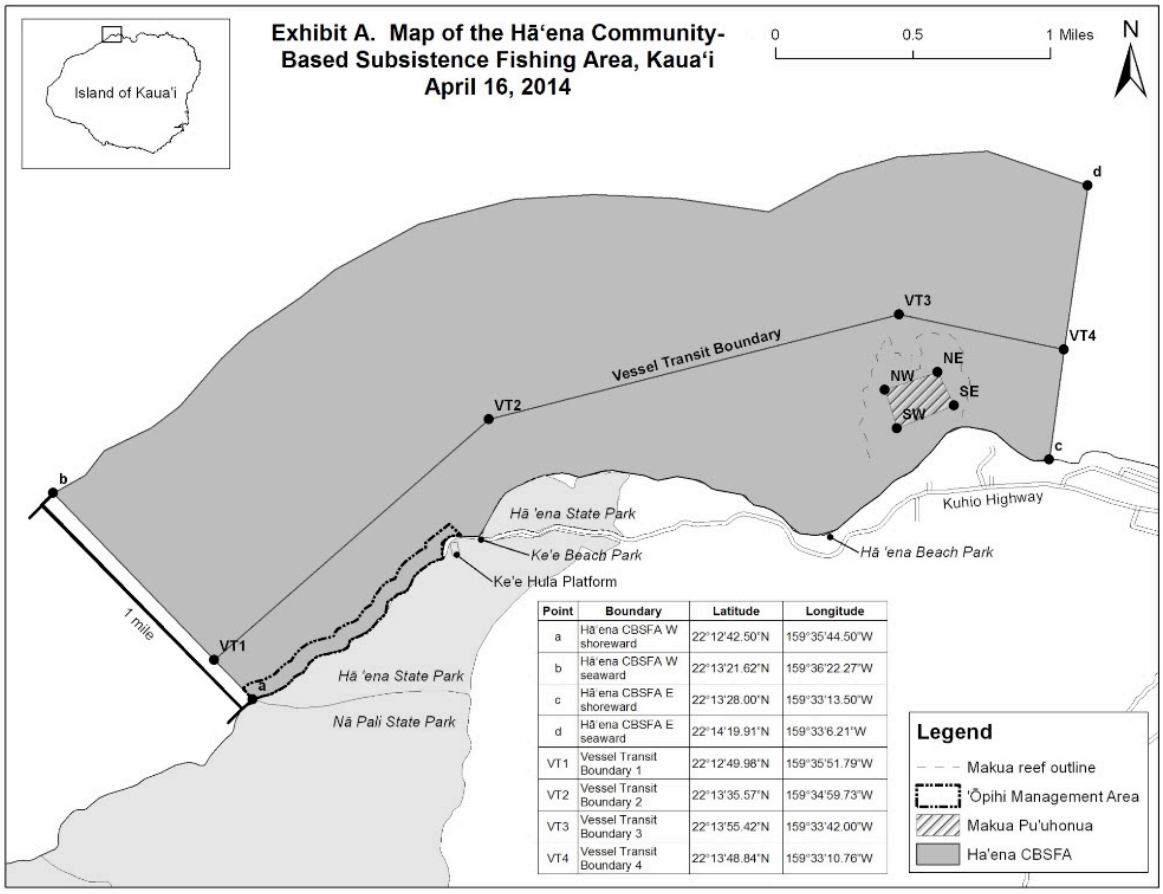

Figure 4. Boundaries and management regimes of the Hā‘ena CBSFA (Rodgers et al. 2017; 2018; 2019).

Hā‘ena is exposed to high wave energy and flushing, especially in the winter months, and is composed of clearly visible coral reef structures in the shallow nearshore environments that can be classified into nearshore, backreef, and forereef habitats. The deeper depths extend beyond the forereef and can be classified as offshore reefs. The reef structures viewed by google earth inside the CBSFA is fairly similar to that east of the boundaries.

A network of streams enters the ocean, both within and outside of the CBSFA boundaries. In spring 2018 the Hā‘ena community experienced a major flooding event following heavy rainfall, which caused a lot of destruction. Although it is typical for Hā‘ena to receive ample rainfall, this event was the worst natural disaster to occur on Kaua‘i in the 25 years since

Hurricane Iniki. The 2018 event exceeded any of the long-standing records for rainfall in a 24-hour period in the Hawaiian Islands. The National Weather Service reported 1,262 mm (49.69 inches) of precipitation at the rain gauge about a mile west of Hanalei Bay near Hā‘ena during April 15-16. The 2018 event closed the only road that connects the community to the rest of the island for a period of 18 months. Before the road closure, 2,000 visitors on average entered Hā‘ena daily. After the road reopened in June 2019, only 900 visitors were allowed into Hā‘ena daily. The increase of freshwater and change in user population resulted in a nearshore biological shift that was supported by anecdotal reports from the community. The shift included large increases in some species of resource fishes that were leaner compared to prior reports.

3.1.2 Sample design

Sites were stratified by depth, habitat type, and location inside and outside the CBSFA boundaries to allow for full spatial representation (Rodgers et al. 2017; 2018; 2019). Study sites did not include areas near the Nā Pali State Park, where the benthic structure begins to change.

Survey sites in 2016, 2017, and 2018 were pre-determined using a stratified random sample design; > 100 random points were generated in ArcGIS10.6.1 (Fig. 5). Points were overlaid on National Oceanographic and Atmospheric Administration (NOAA) habitat base maps (https://products.coastalscience.noaa.gov/collections/benthic/e97hawaii/data2007.aspx; Rodgers et al. 2017; 2018; 2019). These sites were stratified by depth to include two depth ranges (shallow < 7 m; deep ≥ 7m). In the field, if hazardous conditions were present or the depth range was inconsistent with those identified on the maps, transects were placed within 100 m of the original survey site where these conditions no longer existed. Where surveyors encountered greater than 50% sand, they followed the set depth contour until hard substrate was present. Where no hard substrate was visible, the survey was not conducted.

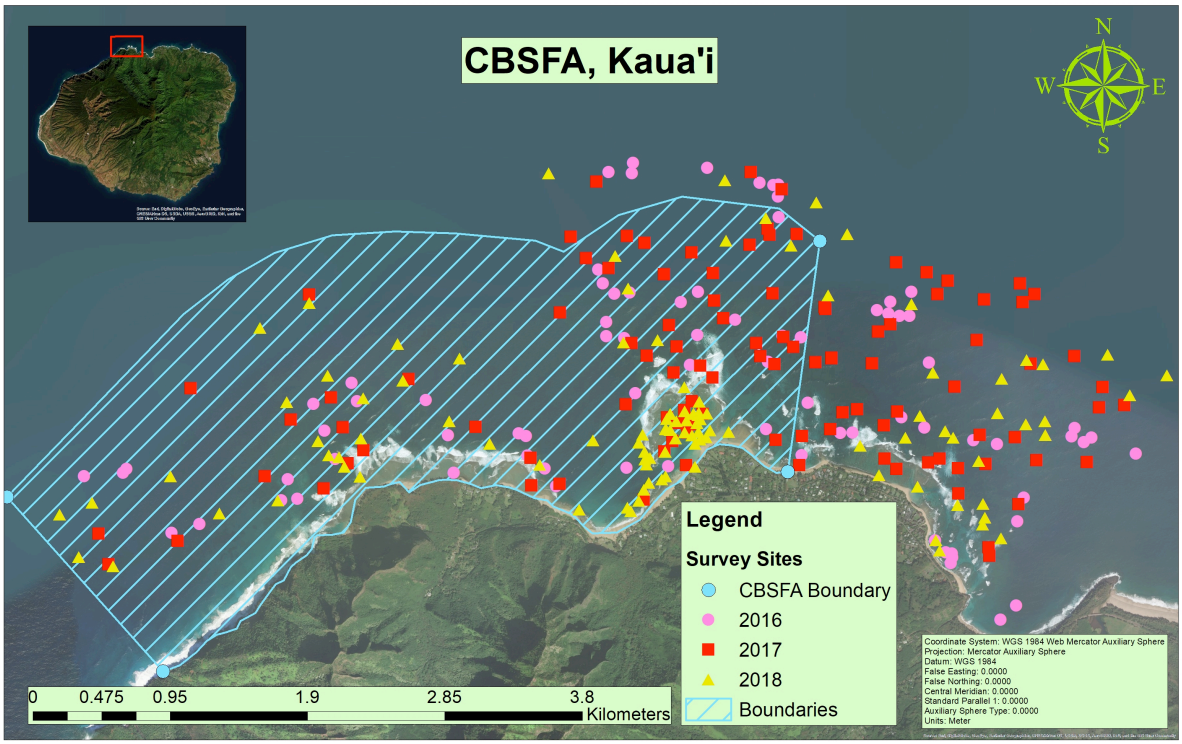

Figure 5. Site locations for years 2016 through 2018 within and outside of the CBSFA boundaries.

3.1.3 Fish surveys

Rapid assessment surveys were conducted using the Kauaʻi Assessments of Habitat Utilization (KAHU) technique (Rodgers et al. 2017; 2018; 2019). Surveys were conducted in August 2016 (n=55 inside, n=43 outside), August 2017 (n=58 inside, n=48 outside), and August 2018 (n=78 inside, n=32 outside) within and outside the CBSFA boundaries. Although surveys were also conducted in June 2017, this data was not included because the number of transects was twice as many in 2017 than for the other years, resulting in an imbalanced distribution of data. For consistency in the time of year (August) when fish surveys were analyzed, the June 2017 data was not subsampled or included.

The KAHU survey techniques were designed from the UH Fisheries Ecology Research Laboratory (FERL) Fish Habitat Utilization Surveys (FHUS), which uses a belt transect method

for estimating fish counts and sizes (Rodgers et al. 2017; 2018; 2019). DAR uses a similar methodology on Maui and O‘ahu.

The survey team was made up of a benthic and fish surveyors (Rodgers et al. 2017; 2018; 2019). All fish surveyors were calibrated by estimating the sizes and counts of the same fishes during calibration dives, as well as by reviewing and discussing the sizes of fishes being surveyed after each dive. Each transect bearing was based on a previously determined cardinal direction that was randomly generated (0°, 90°, 180°, 270°). If the predetermined bearing would not allow the transect to be placed over hard bottom substrate, the surveyor turned clockwise to the next bearing until hard bottom substrate was available for the entire length of the 25 m transect. The fish surveyor laid out the transect line and recorded all fish species, numbers, and sizes (total length [TL cm] within 2.5 m on either side of the transect line for 25 m (125 m^2). The fish surveyor had a minimum of 10-minutes of survey time to account for fast-moving fishes per transect surveyed (Rodgers et al. 2017; 2018; 2019). Maximum time limits were not set.

3.1.4 Benthic surveys

The benthic surveyor remained ~ 7 m behind the fish surveyor so as not to affect fish movement. The benthic surveyor recorded the habitat type that made up > 50% of the visible area in the direction of the transect line from a previously specified list (Table 1). The benthic surveyor also identified and counted species of sea urchins and sea cucumbers that were present within 1 m on either side of the transect line, for 25 m by 2 m (50 m^2). The surveyor simultaneously took photos of the benthic substrate at a 90° angle, 1 m off the substrate at every meter mark along the transect line. The camera was calibrated prior to the survey to assure the same settings. A Cannon S100 camera and underwater housing were secured to a metal monopod with a 1-meter long extension for substrate distance accuracy. Prior to each survey, the white

balance camera function was used for a more realistic adjustment of color at depth. A total of 25 photos were taken at each survey site.

Table 1. A list of benthic habitat type classifications and codes for KAHU surveys.

Habitat Code	Habitat Type	Habitat Description
MIXM	Mixed Medium	Evenly distributed mixture of habitats
PATR	Patch Reef	Patches of coral reef formations seperated by large areas of sand or rubble. Coral cover high on patches.
SAND	Sand	Sand flat made up of sediment with a visual grain size (approx. 0.0625-10 nm)
RUBL	Rubble	Rubble flat made up of limestone or coral rubble/gravel (<25cm in diameter) that is comprised of high rubble to sand ratio
RKBD	Rock/Boulders	Small & Medium rocks to Large boulders, NOT Rubble.
REHO	Reef Hole	Area where a depression exist from the surrounding reef area. Includes Smaller Reef features but not large expansive basin features.
ARTF	Artificial	A structure that cannot be calassified as any other structure that includes harbor pilings or other man-made structures.
COBL	Cobble	Cobble flat made up of limestone or coral cobble (>25cm in diameter) that is comprised of high cobble to sand ratio
SCRUS	Scattered Coral/Rock in Unsonlidated Sediment	Primarily unconsolidated sediment bottom with scattered rocks/boulders or small isolated coral heads that are too small to be delineated individually as patch reefs.
MUD	Mud	Sediment that is too dificult or impossible to determine grain size visually.
PAVE	Pavement	Largely flat, low relief areas with low complexity and relatively low coral cover; dominated by flat limestone or basalt substrate
PAVL	Pavement w/ ledges	Largely flat, low relief areas with low complexity and relatively low coral cover; dominated by flat limestone or basalt substrate with defined overhangs and pronounced ledges
PAVS	Pavement w/ sand channels	Largely flat, low relief areas with low complexity and relatively low coral cover; dominated by flat limestone or basalt substrate with defined sand or rubble channels.
SPGR	Spur & Groove	Ridges of reef formed by corals separated by defined channels "grooves" which often have sediment or rubble bed. Found mostly on forereefs which are exposed to moderate wave energy.
AGRE	Aggregate Reef	Substrate largely dominated by high coral cover with moderate to high complexity.

3.2 L_{50} values

This study used L_{50} values as the parameter for assessing the reproductive maturity of surveyed individuals. L_{50} values are known to vary by location (Schemmel and Friedlander 2017) due to temperature and other ecological influences (Fromentin and Fonteneau 2001; Kaiser et al. 2007). Thus, resource fishes with L_{50} values from the MHI were used to minimize these effects.

L_{50} values in standard length (SL) or fork length (FL) were converted to total length (TL) in cm using the FishBase.org conversions for each species. Female L_{50} values were chosen over male reproduction values because females tend to reach maturity at larger sizes than males (Eble et al. 2009; Nadon 2014; DeMartini and Howard 2016).

Although L_{50} values are an estimate for assessing reproductive maturity in a population of the species of interest, the time at which an individual reaches reproductive maturity may vary by site, year, and season. L_{50} values were acquired mostly through published literature and reports that derived L_{50} values for each species of fish from the MHI whenever possible (Appendix 1). The L_{50} value for convict tang (*Acanthurus triostegus*) was derived from Hā‘ena, while most others were derived from studies and gonad measurements conducted elsewhere in the MHI. For a few species of fish, L_{50} values from the Northwestern Hawaiian Islands were taken from previously published work (Nadon 2017). With the exception of L_{50} values for *Kyphosus* spp. that were derived from a study in Papua New Guinea, species of resource fishes where L_{50} values were not available or originated from locations other than the MHI were not included in this study.

3.3 Statistical analysis

Fish count and size (TL in cm) data from 2016, 2017, and 2018 CREL/DAR datasets were used in this analysis. Within each of these data sets, species that were considered to be resource fishes by the Hā‘ena community’s list (Appendix 2) were removed for further analysis. L_{50} values were acquired for as many of the resource fishes as possible based on the methods stated above.

3.3.1 Permutation-based multivariate analysis of variance

One goal of the study was to determine if resource fish assemblages differed by year and/or by location (inside or outside the CBSFA). Therefore, data used in these subsequent analyses consisted only of resource fish species. All data was inputted into the R statistical software where biomass (g/m^2) and abundance ($number/m^2$) values were initially calculated. Biomass was calculated by first converting total length to standard length and then using the following equation to determine wet weight:

$$W = a\ x\ (\text{standard length})^b$$

a and *b* are parameters for each species of fish that have been estimated by the Hawai‘i Cooperative Fishery Research Unit and/or other researchers. Other parameters and groupings were then added to the original data set, including family level, endemism, trophic levels, L_{50} values, and whether each individual was “above” or “below” its respective L_{50} cutoff.

Multiple transformations were attempted with the biomass and abundance data, yet no transformations resulted in a normal distribution. Therefore, permutation-based multivariate analysis of variance (PERMANOVA) was used to test for resource fish biomass assemblage structure. A PERMANOVA was conducted to assess whether there were any significant differences in the assemblage structure by year and location, and the interaction of the two. The SIMPER test in the “vegan” package in R was used to assess similarity percentages to observe which species had the most influence on the differences observed by the PERMANOVA.

Non-metric multidimensional scaling (nMDS) was used to visualize assemblage structure. The biomass data were square root transformed when calculating distance matrices as a way to down-weight large values in the dataset. The nMSD was applied to fish biomass values with a Bray-Curtis dissimilarity calculation to assess species assemblage structure. An nMDS is

an ordination technique that collapses multiple dimensions into only a few, using rank orders. After viewing stress levels, it was determined that two dimensions would be sufficient.

3.3.2 Test for L_{50} inside vs. outside the CBSFA

The abundance of resource fishes with individuals above their respective L_{50} values inside and outside the CBSFA was compared using a one-tailed t-test. To conduct this analysis, the abundance of resource fishes above their respective L_{50} values was averaged among all three years for each species by location. A one-tailed t-test was chosen to assess differences between locations for each species because the assumption was that assemblage metrics should increase within the MPA over time, relative to the open area.

The t-test did not assess overall distribution, but rather the number of individuals above their respective L_{50} values. This t-test was run with average abundance values from three years of data (n = 3: 2016, 2017, 2018 data). Normality is assessed by the distribution of residuals in a fitted model. Since this one-tailed t-test was based on an n = 3, fitting a distribution was not possible. All species, no matter how rare or abundant, were tested based on n = 3. Therefore, power from the statistical test was equivalent among species.

As this one-tailed t-test was run on multiple species, statistically it was likely to produce at least one false statistically significant ($p \leq 0.05$) outcome by chance alone (Rice 1989). Considering 14 one-tailed t-tests were run, it is likely that several of these significant outcomes ($p \leq 0.05$) resulted from Type-I statistical error (Rice 1989). Yet, studies have shown that as long as the effect of size is large with low sample sizes ($n \leq 5$), Type-I error rates were roughly 5% with statistical power remaining fairly high at 80% (de Winter 2013). Although the determined significance values were promising, these results should be viewed for the overall trend that it displays for each species (de Winter 2013).

3.3.3 Generalized linear models

The purpose of this analysis was to identify whether resource fishes were significantly ($p < 0.05$) associated with certain habitat types inside or outside the CBSFA boundaries. Due to non-normal distributions of biomass, a generalized linear mixed model was used to test these relationships. Unplanned comparisons between pairs were examined using the Tukey-Kramer HSD (honestly significant difference) to directly test the relationship between specific species and their habitat associations among locations.

The species of resource fishes in < 5% of the total transects were excluded before the analysis, and natural log-transformed biomass values were used as the dependent variable. This transformation allowed a better fit of the model and the distribution of the residuals were scattered to meet the generalized linear model assumptions. After fitting the model and assessing the residual distributions and scatter, inverse gamma distribution with the transformed dependent variable was fairly well scattered and normally distributed. Hence, the gamma distribution with an inverse link function was used.

A generalized linear model can mix continuous variables with categorical variables to identify interactions. The data must be independent, but the dependent variable did not need to be normally distributed, homogeneity of variance was not necessary, and a linear relationship between the dependent and independent variables was not assumed (Jiao and Chen 2004; Venables and Dichmont 2004). The gamma distribution is one where the mean was expected to equal the variance and is one of assumed exponential pattern with the data (Jiao and Chen 2004; Venables and Dichmont 2004). Pairwise Tukey comparisons followed the model to test for specific combinations of associations (Jiao and Chen 2004; Venables and Dichmont 2004).

Natural log-transformed biomass values were used as the dependent variable and location (inside or outside the CBSFA), year, depth, and habitat type as a fixed effect, additive variables. The relationships between species biomass and where they were surveyed allowed for conclusions to be made about the habitats in which resource fishes were surveyed. Pairwise comparisons were observed after fitting the generalized linear model to view specific relationships of biomass-habitat associations.

CHAPTER 4. RESULTS

Resource fish species were recorded on a total of 261 (83%) out of the 314 transects surveyed between all three years—August 2016, August 2017, August 2018. Resource fishes were observed on 64% of transects inside the CBSFA and 36% outside the CBSFA boundaries (Table 2). Since 2016, the number of transects where resource fish species were found has been increasing inside the CBSFA but has varied outside the CBSFA.

Table 2. Total number of transects with resource fish species by year and location. Transect percentages out of the total 261 sites are recorded in parentheses.

Year	Inside	Outside	TOTAL
2016	48 (18%)	30 (11%)	78 (30%)
2017	53 (20%)	37 (14%)	90 (34%)
2018	66 (25%)	27 (10%)	93 (36%)
TOTAL	167 (64%)	94 (36%)	**261**

4.1 Resource fish assemblages

A total of 29 of the 49 species of resource fishes from the Hā‘ena community list (Appendix 2) were observed at least once during the three years of surveys. These 29 species comprised 9 families with 9,431 individuals (Appendix 1). Statistical analyses excluded species of fish found in less than 13 (~5%) of 261 transects, resulting in a total of 19 resource fish species (Appendix 3). The following statistical analyses refer to these 19 species of resource fishes only. Species excluded tended to be either the more mobile, cryptic, and/or rare species of fishes. Species that occurred in > 5% of the total transects made up ~ 98.0% of the total abundance and 96.4% of the total biomass.

The most abundant species surveyed during the 3-year span included *Acanthurus triostegus* (*manini*; 24.4%), *Kyphosus* spp. (*nenue*; 16.1%), *Lutjanus kasmira* (*ta'ape*; 9.7%), *Scarus rubroviolaceus* (*palukaluka*; 4.4%), and *Mulloidichthys vanicolensis* (*weke 'ula*; 8.1%). These top five species comprised 62.7% of the total abundance and 71.6% of the total biomass of the overall resource fish assemblage for the 19 species (Table 3). The most frequently observed fishes by percent frequency of occurrence on transects were *A. triostegus* (*manini*; 53%), *S. rubroviolaceus* (*palukaluka*; 45%), *Naso lituratus* (*umaumalei*; 40%), *Naso unicornis* (*kala*; 40%), and *Kyphosus* spp. (*nenue*; 28%).

Table 3. Resource fish species that occurred in more than 13 (5%) of total transects for statistical analysis. The percentage of the total abundance, biomass, and frequency of occurrence (by the number of transects (for each species observed).

Scientific Name	Common Name	Hawaiian Name	% Total Abundance	% Total Biomass	% Frequency of Occurance
*Acanthurus triostegus**	Convict Tang	manini	24.4	5.6	53
*Kyphosus species**	Lowfin Chub	nenue	16.1	9.9	29
Lutjanus kasmira	Bluestripe Snapper	ta'ape	9.7	6.8	20
*Scarus rubroviolaceus**	Redlip Parrotfish	palukaluka	4.4	45.1	45
*Mulloidichthys vanicolensis**	Yellowfin Goatfish	weke 'ula	8.1	4.2	6
Naso lituratus	Orangespine Unicornfish	umaumalei	5.5	4.7	40
*Naso unicornis**	Bluespine Unicornfish	kala	4.9	6.0	40
Acanthurus blochii	Ringtail Surgeonfish	pualu	4.6	2.8	26
*Mulloidichthys flavolineatus**	Yellowstripe Goatfish	weke	3.6	0.7	5
Monotaxis grandoculis	Bigeye Emperor	mu	3.0	3.3	15
*Caranx melampygus**	Blue Trevally	'omilu	2.3	2.5	28
*Acanthurus nigroris**	Bluelined Surgeonfish	maiko	1.7	0.4	15
*Acanthurus dussumieri**	Eye-stripe Surgeonfish	palani	1.3	1.1	20
Parupeneus cyclostomus	Blue Goatfish	moano kea	0.9	0.6	17
*Scarus psittacus**	Palenose Parrotfish	uhu	0.5	0.5	5
Cephalopholis argus	Blue-spotted Grouper		0.8	1.0	17
*Calotomus carolinus**	Stareye Parrotfish		0.5	0.3	11
Lutjanus fulvus	Blacktail Snapper	to'au	0.5	0.2	9
Aprion virescens	Green Jobfish	uku	0.3	0.7	7

* = Hā'ena species list

4.1.1 Permutation-based multivariate analysis of variance

Results of PERMANOVA indicated that location explained ~27% of the variance in resource fish assemblage structure, but was not significant ($p = 0.10$; $df = 1$). Although survey years were included in the model and explained ~37% of species biomass variance ($p = 0.03$; $df = 1$), location was the only variable that successfully produced homogenous dispersion. The interaction term between year and location was not significant ($p = 0.57$; $df = 1$) and explained only ~10% of the variance.

SIMPER results indicated that *Scarus rubroviolaceus* was the species most responsible for the difference in biomass among years (Table 4a), location (Table 4b), and habitat (Table 4c). The second and third species that most contributed to the differences were variable by year, location, and habitat types.

Table 4a. SIMPER results for the top three species between year comparisons.

	Top Species	**Average Biomass (g/m^2)**	**Standard Deviation**
2016 - 2017	*Scarus rubroviolaceus*	0.043	0.036
	Aprion virescens	0.024	0.021
	Naso unicornis	0.022	0.02
2016 - 2018	*Scarus rubroviolaceus*	0.045	0.034
	Caranx melampygus	0.021	0.02
	Aprion virescence	0.021	0.02
2017 - 2018	*Scarus rubroviolaceus*	0.042	0.039
	Naso unicornis	0.021	0.018
	Monotaxis grandoculis	0.018	0.014

Table 4b. SIMPER results for the top three species between location comparisons.

	Top Species	**Average Biomass (g/m^2)**	**Standard Deviation**
Inside - Outside	*Scarus rubroviolaceus*	0.041	0.036
	Caranx melampygus	0.021	0.018
	Naso unicornis	0.019	0.017

Table 4c. SIMPER results for the top three species between habitat type comparisons.

	Top Species	Average Biomass (g/m^2)	Standard Deviation
Aggregate Reef - Mixed	*Scarus rubroviolaceus*	0.038	0.027
	Cephalopholis argus	0.021	0.011
	Caranx melampygus	0.02	0.014
Aggregate Reef - Pavement	*Scarus rubroviolaceus*	0.025	0.023
	Aprion virescence	0.018	0.015
	Parupeneus cyclostomus	0.013	0.008
Aggregate Reef - Rock & Boulder	*Scarus rubroviolaceus*	0.044	0.03
	Caranx melampygus	0.024	0.014
	Naso unicornis	0.02	0.017
Aggregate Reef - Spur & Groove	*Scarus rubroviolaceus*	0.041	0.03
	Naso unicornis	0.019	0.016
	Lutjanus kasmira	0.019	0.015
Mixed - Pavement	*Scarus rubroviolaceus*	0.048	0.026
	Monotaxis grandoculis	0.023	0.01
	Cephalopholis argus	0.022	0.012
Mixed - Rock & Boulder	*Scarus rubroviolaceus*	0.048	0.046
	Naso unicornis	0.026	0.021
	Caranx melampygus	0.025	0.027
Mixed - Spur & Groove	*Scarus rubroviolaceus*	0.045	0.044
	Naso unicornis	0.025	0.021
	Caranx melampygus	0.021	0.022
Pavement - Rock & Boulder	*Scarus rubroviolaceus*	0.046	0.027
	Caranx melampygus	0.026	0.004
	Monotaxis grandoculis	0.026	0.01
Pavement - Spur & Groove	*Scarus rubroviolaceus*	0.043	0.031
	Monotaxis grandoculis	0.022	0.013
	Aprion virescence	0.021	0.019
Rock & Boulder - Spur & Groove	*Scarus rubroviolaceus*	0.053	0.048
	Naso unicornis	0.022	0.021
	Caranx melampygus	0.017	0.024

The nMDS ordination results demonstrated that sites within the CBSFA had higher concordance than outside the CBSFA (Fig. 6). High *Scarus psittacus* biomass was significantly correlated with sites inside the CBSFA, while high *S. rubroviolaceus* biomass was significantly correlated with sites outside the CBSFA (Fig. 6). There was a moderate correlation ($0.05 < p > 0.1$) of *Cephalopholis argus*, *Naso unicornis*, and *Lutjanus kasmira* with high biomass outside the CBSFA boundaries between 2017 and 2018 survey years (Fig. 6). Although correlations were weak and not significant, the rest of the resource fishes were fairly evenly distributed according to biomass by location.

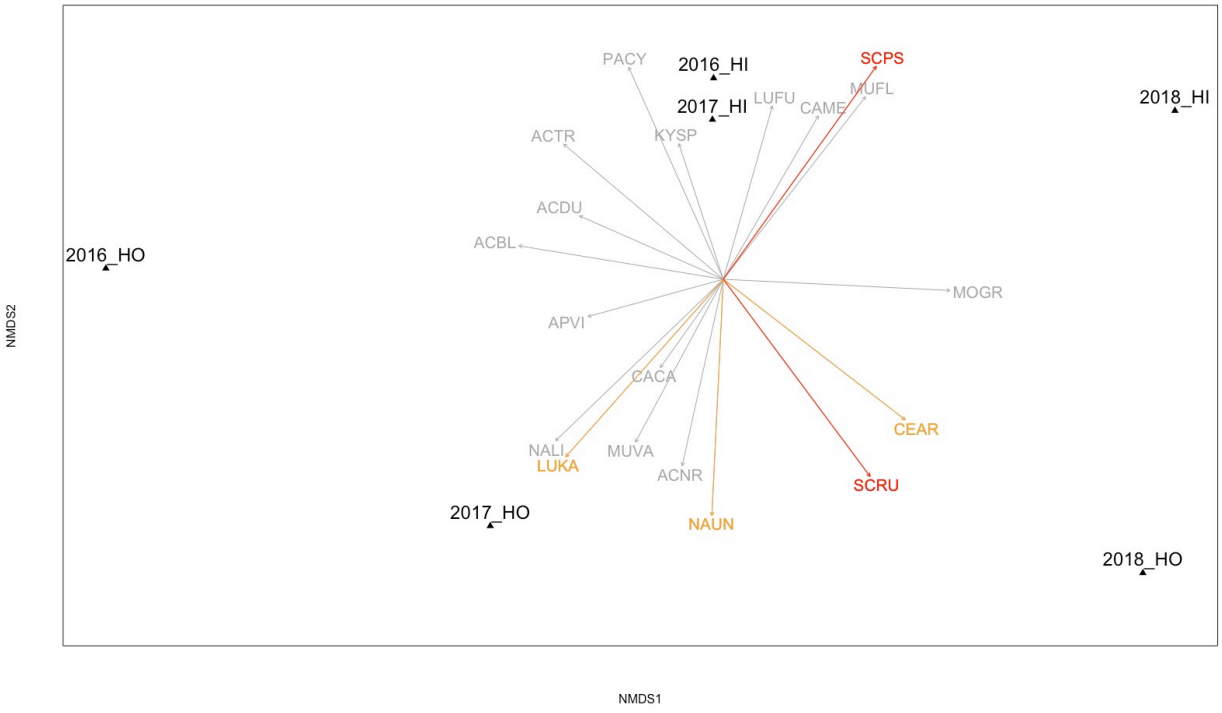

Fig. 6. nMDS ordination plot of the distribution of resource fish biomass among each year and location. Resource fish species are represented by vectors; red* highlights indicating strong correlation ($p < 0.05$) and orange highlights indicating acceptable correlation ($0.05 < p < 0.1$) to year and location. *SCPS = *Scarus psittacus*, *SCRU = *Scarus rubroviolaceus*, CEAR = *Cephalopholis argus*, NAUN = *Naso unicornis*, LUKA = *Lutjanus kasmira*.

4.2 Reproductively mature resource fishes

Comparison of average abundances of resource fish species individuals above their L_{50} values resulted in 4 out of 14 species with significant ($p < 0.05$) differences inside versus outside the CBSFA boundaries (Figure 7). These species were *Acanthurus triostegus* ($p = 0.03$; $df = 2$), *Cephalopholis argus* ($p = 0.03$; $df = 2$), *Parupeneus cyclostomus* ($p = 0.03$; $df = 2$), and *Scarus rubroviolaceus* ($p = 0.05$; $df = 2$).

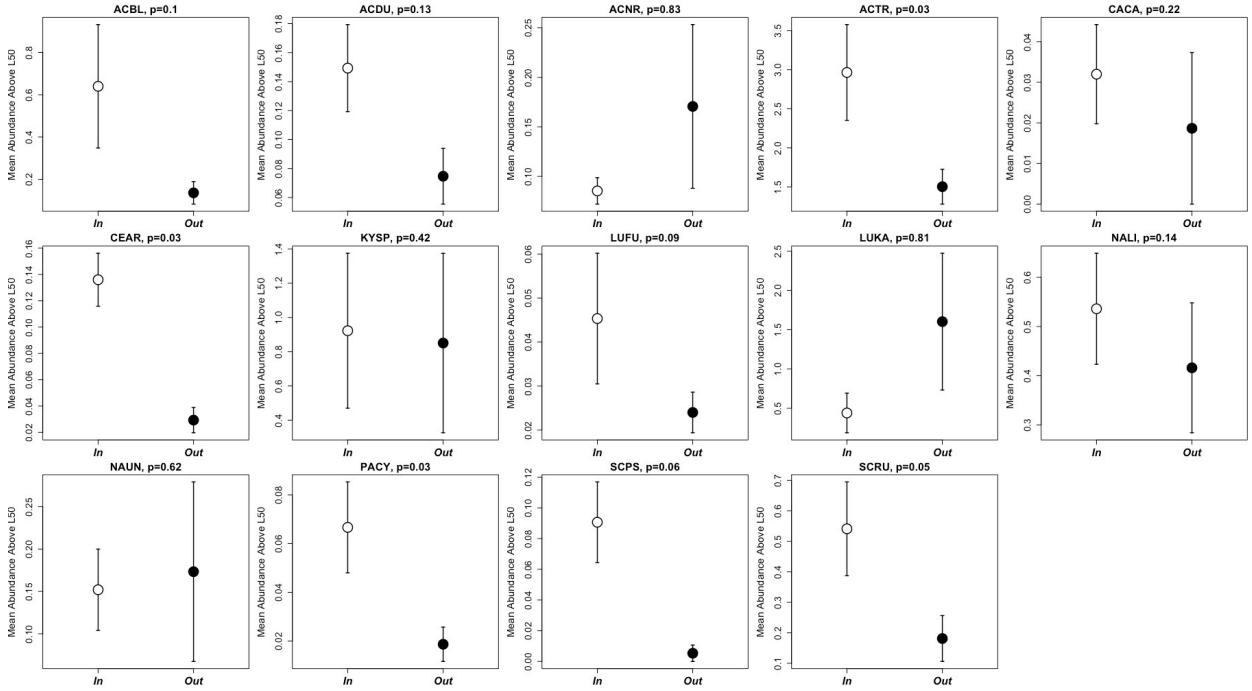

Fig. 7. One-way t-test of mean abundance of resource fish species individuals above their respective L_{50} values inside and outside the CBSFA boundaries. The asterisks (*) represent species with significant differences. ACBL = *Acanthurus blochii*, ACDU = *A. dussumeiri*, ACNR = *A. nigroris*, *ACTR = *A. triostegus*, CACA = *Calotomus carolinus*, *CEAR = *Cephalopholis argus*, KYSP = *Kyphosus* spp., LUFU = *Lutjanus fulvus*, LUKA = *L. kasmira*, NALI = *Naso lituratus*, NAUN = *N. unicornis*, *PACY = *Parupeneus cyclostomus*, SCPS = *Scarus psittacus*, and *SCRU = *S. rubroviolaceus*.

4.3 Resource fish-habitat associations

Out of the 261 total sites surveyed, five different types of habitat were recorded for each year, by location (Table 5). For each year (2016, 2017, 2018), there were more surveys

conducted inside the boundaries as opposed to outside the CBSFA. Furthermore, survey sites with pavement habitat types were the most abundant, with aggregate reef as the second most abundant habitat type (Table 5).

Table 5. Number of transects with habitat type allocations by year and location. Percentages of sites out of the total number of sites per year surveyed are recorded in parentheses.

Year	Habitat	Inside	Outside	TOTAL
2016	Aggregate Reef	16	10	26 (33%)
	Mixed	7	2	9 (12%)
	Pavement	18	9	27 (35%)
	Rock Boulder	1	3	4 (5%)
	Spur and Groove	6	6	12 (15%)
	SUB-TOTAL	48	30	78
2017	Aggregate Reef	15	5	20 (22%)
	Mixed	-	1	1 (1%)
	Pavement	38	31	69 (77%)
	Rock Boulder	-	-	-
	Spur and Groove	-	-	-
	SUB-TOTAL	53	37	90
2018	Aggregate Reef	25	-	25 (27%)
	Mixed	2	4	6 (6%)
	Pavement	34	21	55 (59%)
	Rock Boulder	-	2	2 (2%)
	Spur and Groove	5	-	5 (5%)
	SUB-TOTAL	66	27	93
TOTAL		167	94	**261**

The first examination at effects after fitting the Generalized Linear Model (GLM) revealed that year had little effect on the distribution of biomass among locations and habitats. Resource fish biomass outside the CBSFA was significantly higher ($p = 0.008$) than the biomass inside the CBSFA (Fig. 8). The fixed effect of depth revealed that deeper sites had significantly higher biomass than shallower sites ($p = 0.002$; Fig. 9). In terms of resource fish biomass among habitat types, pavement reef habitats had significantly higher biomass ($p < 0.001$; Fig. 10) than rock-boulder, spur-and-groove, aggregate, and mixed habitat types (in the order of highest to

lowest biomass comparisons). Pairwise comparisons between habitats revealed that between species biomass among locations combined, pavement reef habitats had significantly higher biomass than aggregate reef habitats ($p < 0.001$; Fig 11.).

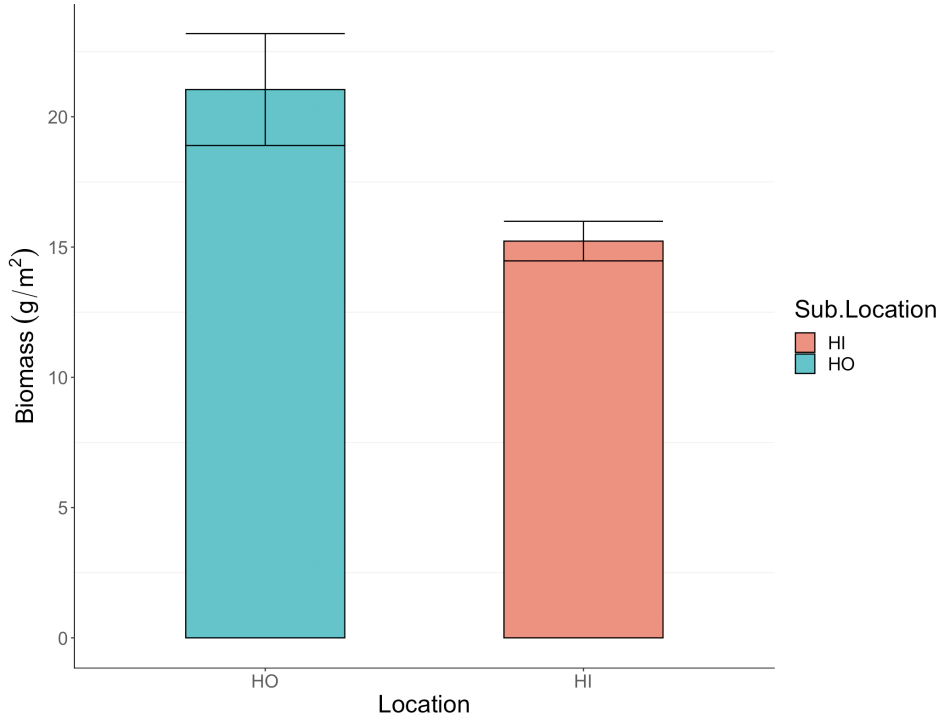

Figure 8. Generalized linear model results showing significantly larger biomass values outside (HO) the Hā‘ena CBSFA compared to inside (HI).

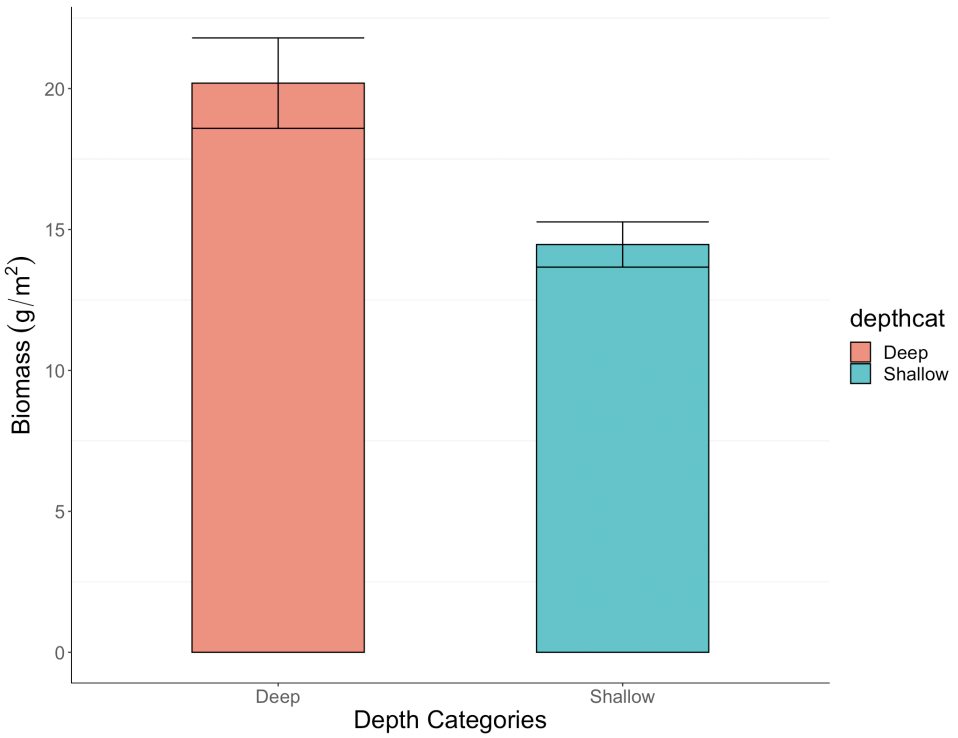

Figure 9. Generalized linear model results showing significantly larger biomass values at deeper sites compared to shallower sites.

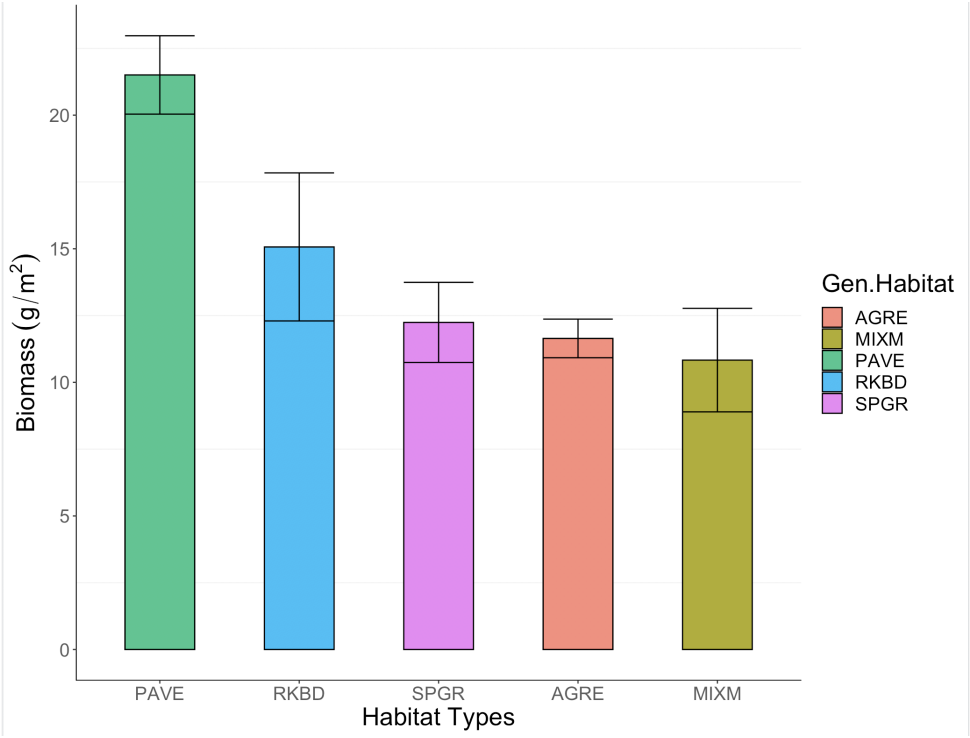

Figure 10. Generalized linear model results showing significantly larger biomass values among pavement (PAVE) habitats in relation to rock-boulder (RKBD), spur and groove (SPGR), aggregate reef (AGRE), and mixed (MIXM) habitat types.

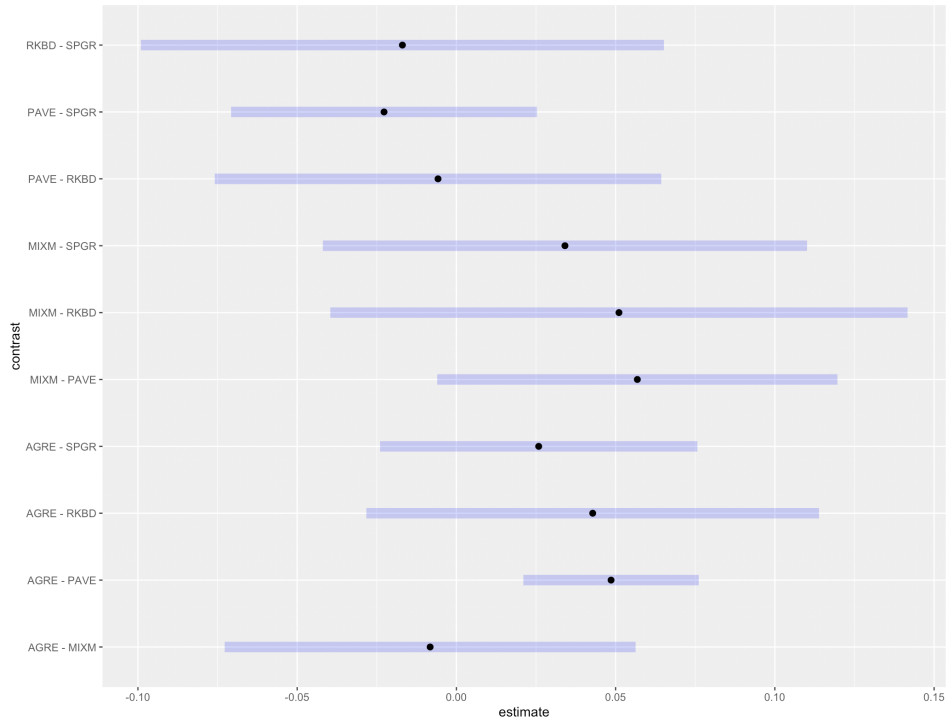

Figure 11. Pair-wise comparison confidence intervals of the Generalized Linear Model (GLM) results showing significantly larger biomass values at pavement (PAVE) habitats in relation to aggregate reef (AGRE) habitats. The rest of the habitat type comparisons were not significant among rock-boulder (RKBD), spur and groove (SPGR), and mixed (MIXM) habitat types.

Pair-wise comparisons between location, habitat type, and fish species show that most interactions and combinations were not significant. However, for all 19 species of resource fishes tested, pavement reef habitats inside the CBSFA had significantly higher biomass of resource fishes than aggregate reef habitats outside of the CBSFA (Appendix 4). Tests also determined that biomass for all 19 species inside the CBSFA boundaries was higher in pavement habitats as opposed to aggregate reef habitats inside the boundaries, and the same conclusions were found when comparing aggregate habitats to pavement habitats outside the boundaries (Appendix 4).

CHAPTER 5. DISCUSSION

Understanding how the abundance and biomass of fishes are distributed across coral reefs and varying habitat types can provide valuable insight into optimal management of nearshore coral reef ecosystems (Friedlander and Parrish 1998; Gratwicke and Speight 2006; Wedding and Friedlander 2008; Magris et al. 2016). This knowledge is especially beneficial when an adaptive management strategy is employed, such as with the Hā‘ena CBSFA, which allows for an adaptation of rules and regulations to meet the needs of the ecosystem and the local community (Agardy 2000).

The objectives of this study were to examine resource fish assemblages inside and outside the CBSFA, determine whether or not the reproductively mature resource fishes have increased inside the CBSFA over the past three years, and identify fish-habitat associations to determine which habitats contained the highest biomass. Several hypotheses that could explain the results of this study are discussed below: 1) the CBSFA has no effect on the biomass of fishes inside the CBSFA; 2) there has been insufficient time for resource species to respond to restrictions on fishing gear that were initiated in 2015; 3) habitats are different inside and outside the CBSFA; 4) the CBSFA is too small and does not contain habitats that adequately protect resource fish species; 5) poaching is occurring within the CBSFA; and 6) low statistical power due to small sample sizes limited the ability to discern actual differences.

5.1 CBSFA effectiveness

There is a possibility that these results suggest the ineffectiveness of the CBSFA over the last three years. *Acanthurus triostegus* and *Kyphosus* spp. were among the most abundant taxa overall. Biomass of an important parrotfish species, *Scarus psittacus*, was positively correlated

within the CBSFA. Another important parrotfish species, *Scarus rubroviolaceus*, had higher numerical abundance inside the CBSFA, but biomass, hence larger individuals, was correlated with areas outside the CBSFA, particularly in 2018. If juveniles remained within the CBSFA, then biomass of this species would be expected to increase over time.

The lack of significant patterns in biomass and abundance after three years of data collection could indicate that the CBSFA has been simply unsuccessful. However, it is possible that three years is insufficient time for resource fisheries to respond to the rules and restrictions on fishing gear within the CBSFA. The Kahekili Herbivore Fisheries Management Area (KHFMA) is an example of an MPA on the island of Maui that protected herbivorous fisheries (Williams et al. 2016). The study reviewed the effectiveness of the MPA after six years of protection (Williams et al. 2016). These results indicated a higher biomass of herbivorous fishes that resulted in increased crustose coralline algae and decreased macroalgae cover (Williams et al. 2016). The KHFMA also had strict no-fishing restrictions on herbivorous species, whereas the CBSFA allows fishing of resource fishes with limitations on fishing gears used. Therefore, three years may simply be insufficient time to observe changes in resource fish abundances and biomass, as it would take longer to observe effectiveness when restrictions are purely fishing gear-related, as opposed to strict no fishing rules and regulations.

A study on the Great Barrier Reef tracked the density of coral trout within no-take reserves and in fished areas over an eight-year period (Williamson et al. 2014). Results from this study were affected by two disturbances: a coral bleaching event and a prolonged freshwater plume (Williamson et al. 2014). Although the disturbances caused an overall decrease in coral trout densities, the no-take reserves consistently maintained higher densities than fished areas, indicating the importance of no-take reserves as a refuge and recovery areas from major

disturbances (Williamson et al. 2014). Again, this study reviewed effectiveness after eight years of data collection, as opposed to only three years in the Hā‘ena CBSFA. However, similarly to this Great Barrier Reef study, the Hā‘ena CBSFA experienced a major 2015 bleaching event as well as a major flooding event in early 2018 that may have had indirect effects on fish biomass and abundances within the CBSFA. The Great Barrier Reef study found that the bleaching event and prolonged freshwater plume negatively affected coral cover and benthic complexity, which indirectly affected fish abundance and diversity (Williamson et al. 2014). These major disturbances in Hā‘ena were not studied in detail and are beyond the scope of this thesis. As future surveys in the Hā‘ena CBSFA continue, it is crucial to keep these disturbance events in mind, as they may have affected the results of the CBSFA surveys over the last three-year period.

Models revealed that yearly differences accounted for very little of the variability in biomass that was observed by location ($p = 0.109$) and habitat ($p = 0.304$). This also suggests that three years may not be enough for the CBSFA rules and regulations to have had a major effect on fish biomass, or that the rules and regulations for some species, and possibly their habitat associations, may need adapting.

5.2 Habitat variations and size

Habitat selection by fishes is dependent on stages of life cycles, shelter for vulnerable species, feeding preferences, and nocturnal behaviors (Sudekum et al. 1991; Friedlander et al. 2007b; Howard et al. 2008; Jones et al. 2010; Berglund et al. 2012; Graham and Nash 2013; DeMartini and Howard 2016; Chung et al. 2019; Friedlander et al. 2019; Wedding et al. 2019). Typically, aggregate reef habitats that provide higher benthic complexity and structure for

individuals to take shelter from predation hold higher biomasses, abundances, and diversity of fish species (Graham and Nash 2013; Wedding et al. 2019). However, results from this study indicated biomass was significantly higher in pavement habitats in comparison to aggregate reef habitats. This could be due to a higher number of transect sites that were recorded as pavement habitats *in situ*, as opposed to a lower number of sites within the other four habitat types (Table 5).

As mentioned in the methods section, transect sites were randomly chosen and stratified by depth to provide an even number of shallow and deep sites within and outside of the CBSFA. Benthic structure compatibility between inside and outside the boundaries when determining survey sites was purely based on visual interpretation of Google earth images and NOAA benthic habitat map overlay. *In situ* observations of habitat types were not consistent with ArcGIS predictions of evenly distributed habitat types. Future surveys may need to reassess survey sites in relation to equal habitat types, in addition to equal depth stratifications, in order to provide a more complete and balanced representation of habitat types within and outside of the CBSFA. Overlaying NOAA benthic habitat maps with LiDAR (Light Detection and Ranging) and *in situ* observer interpretation of habitat types prior to conducting future surveys may provide a more thorough representation of equal habitat types within and outside the CBSFA.

The high abundances of *S. rubroviolaceus* inside the CBSFA boundaries, yet higher biomass of the same species outside of the boundaries suggests that 1) the larger individuals outside the CBSFA may be supplying the CBSFA with fish recruits, 2) the habitats outside of the CBSFA are more conducive to the larger *S. rubroviolaceus* individuals, and 3) the habitats inside of the CBSFA—possibly the Makua Pu‘uhonua—are more conducive to smaller and younger *S. rubroviolaceus* individuals that have not likely reached reproductive maturity. If larger

individuals of certain species prefer habitat types outside of the CBSFA, then it may be necessary to consider enlarging CBSFA boundaries.

Furthermore, taking into consideration the life span of several of these species of resource fishes and how quickly they reach reproductive maturity can have implications on how long and for what stages habitat types may be valuable to individuals. For example, *Naso unicornis* life span is roughly 50 years and they begin reproducing on average at 2.9 years of age; *Scarus rubroviolaceus* reaches roughly 22 years and reproduces on average at 3 years of age; *Caranx melampygus* reaches roughly 7 years and reproduces on average at 2.1 years of age (Nadon 2017). As the species listed above begin reproducing at roughly 3 years of age, there may have been several ontogenetic shifts occurring for certain individuals during this period of surveys. Several more years' worth of data may provide clear and stabilized patterns in habitat selection to emerge.

Although the Hā‘ena CBSFA is not strongly or fully protected against fishing, it is one of the larger MPAs in the state of Hawai‘i at roughly 8 km^2, which is larger than the median sized (1.2 km^2) MPAs in the state. Yet, taking into consideration how large MPAs need to be in order to be effective—roughly 10 to 100 km^2 (Gaines et al. 2010)—the Hā‘ena CBSFA is still well below that threshold. Although expanding the CBSFA would be difficult because of political pushback, it may be possible to aim for establishing networks of MPAs surrounding the Hā‘ena CBSFA that would incorporate variety and redundancy of varied habitat types. In this manner, a wider range and frequency of habitat types may provide better protection via redundancy in habitat types, as well as sustaining larval recruitment between MPAs (Gaines et al. 2010; Berglund et al. 2012). Further research into larval recruitment of resource fish species in the

Hā‘ena region would provide valuable insight into the self-sustaining effectiveness of the Hā‘ena CBSFA.

5.3 Limitations

Poaching is a threat to any MPA in the marine environment, especially where enforcement is limited. It has been identified in the KHMFA six-year protection results that low-level poaching in the area may have influenced the low abundances of larger-bodied species that failed to recover fully (Williams et al. 2016). Although the same concerns exist in the Hā‘ena CBSFA, the advantages of community and stakeholder involvement in the area would decrease the level of poaching that occurs.

Small sample sizes for most resource fish species were evident, except for *Acanthurus triostegus*. Especially for rare species, low sample sizes may decrease statistical power and make it challenging to obtain accurate results. In reality, most nearshore fisheries studies are low in sample sizes and typically result in non-parametric statistical analyses that are tailored to such limitations. Even for unfished regions, fish population distributions are naturally skewed to where smaller individuals are more abundant in size, and as they become larger, abundant sizes decrease. Sometimes it is possible to transform the data to run parametric tests, yet there are also robust statistical analyses, such as generalized linear models with Poisson or Gamma distributions, to account for residual normality challenges (Venables and Dichmont 2004). As the data in this study could not be transformed to fit parametric tests, generalized linear models were used and assessed for assumptions.

From a methodological standpoint, the areas within and outside of the CBSFA have been saturated with survey sites to where it would not be possible to run more transects in an attempt

to increase the sample size. A possibility would be to consider conducting surveys two to four times per year to assist in providing higher sample sizes, as well as providing further insight into seasonal variation patterns that may emerge for certain species. Furthermore, continuing to conduct surveys in a study beyond 5 years may be beneficial in discovering long-term patterns that can aid in adaptive management of the rules and regulations.

Finally, L_{50} values can vary not only by location and water temperature but also by season and year (Fromentin and Fonteneau 2001; Kaiser et al. 2007). Although the L_{50} value for *Acanthurus triostegus* came directly from gonad measurements of individuals located around the Hā‘ena area, L_{50} values of most other species were derived from measurements of individuals from the MHI, some from the NWHI, and one from Papua New Guinea (Appendix 1). L_{50} values are the best estimate that can be used to assess reproductive maturity using *in situ* observations. Hence, conducting further research to acquire L_{50} values for all resource fish species from the Hā‘ena region could be beneficial in ensuring precise analyses of that location specifically. Examining resource fish individuals that were larger than their respective L_{50} values from these varied locations made it possible to assess differences. *Acanthurus triostegus*, *Cephalopholis argus*, *Parupeneus cyclostomus*, and *Scarus rubroviolaceus* had reproductively mature individuals that displayed higher abundances inside the CBSFA than outside. It would be interesting to see if acquiring and using L_{50} values from the specific Hā‘ena region would provide different results.

CHAPTER 6. CONCLUSIONS

I examined biomass and abundance of resource fishes within and surrounding the Ha'ena Community Based Subsistence Fishing Area (CBSFA) boundaries in north Kaua'i to better understand whether resource fish species have been increasing since the rules and regulations on fishing gear were initiated in 2015. I also assessed the use of L_{50} values as a proxy for estimating the biomass and abundance of reproductively mature resource fishes.

Results indicated that biomass was significantly higher outside of the CBSFA boundaries, biomass at deeper survey sites was significantly higher than shallower sites, and pavement habitats held significantly higher biomass. *Scarus rubroviolaceus*, in particular, demonstrated higher biomass outside of the CBSFA boundaries, but higher abundances inside the boundaries. This suggests that larval recruitment for *S. rubroviolaceus* is coming from outside the boundaries, and habitat may play a vital role in where larger or smaller individuals of fishes may be located. The abundances of individuals above their respective L_{50} values were evident within the CBSFA for *Acanthurus triostegus* (*manini*; $p = 0.03$; $df = 2$), *Cephalopholis argus* ($p = 0.03$; $df = 2$), *Parupeneus cyclostomus* (*to'au*; $p = 0.03$; $df = 2$), and *Scarus rubroviolaceus* (*pulukaluka*; $p = 0.05$; $df = 2$).

Possibilities for these results were that the CBSFA rules and regulations are not effective, or that there has simply not been enough time for fishes to respond to restrictions on fishing gear. There is also the possibility that the CBSFA is too small and does not incorporate substantial habitat types for resource fish species at multiple stages in their life cycles, or that habitat types within and outside of the CBSFA are simply variable. Poaching may also be a threat to the CBSFA resource fish species. Finally, low sample sizes may play a role in limiting statistical power, influencing the results of this project.

Longer-term monitoring may provide data to allow for more robust analyses in the future. These monitoring data are essential if adaptive changes in rules and regulations are to be implemented in the future. The recommendation of this study is that continuing yearly surveys may allow for long-term trends to emerge that may better predict how resource fishes are changing to further effective management. Furthermore, determining future survey sites that equally represent habitat types within and outside of the CBSFA are crucial in assessing habitat preferences and emerging patterns of resource fish biomass and abundances.

For the Hā‘ena CBSFA to be successful, the local community and managers must hold each other accountable by enforcing rules and regulations. They must also change and adapt the rules and regulations to best meet the needs of marine and community populations. Through this learning process, with the involvement of state agencies and the contribution of local communities to implement adaptive management strategies, other successful CBSFAs could be established in appropriate areas throughout Hawai‘i to create a healthy, sustainable future for all who benefit from these diverse marine ecosystems.

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APPENDIX

Appendix 1. List of resource fish species with sources from which L_{50} values were derived. Species derived from the Hā‘ena resource fish species list are noted with an asterisk (*).

Family	Code	Taxon Name	Common	Hawaiian	L50 (cm)	Citation
Acanthuridae	ACBL	*Acanthurus blochii*	Ringtail Surgeonfish	pualu	27.6	Nadon, Choat and Robertson (2002), Kritzer (2001)
	ACDU	*Acanthurus dussumieri**	Eye-stripe Surgeonfish	palani	28.2	Choat and Robertson (2002), Nadon, Kritzer (2001)
	ACNR	*Acanthurus nigroris**	Bluelined Surgeonfish	maiko	15.7	DiBattista et al. (2010)
	ACTR	*Acanthurus triostegus**	Convict Tang	manini	13.2	Schemmel, Friedlander 2017
	NABR	*Naso brevirostris*	Spotted Unicornfish	kala lolo	26.9	Choat and Robertson (2002), Nadon, Kritzer (2001)
	NAHE	*Naso hexacanthus*	Sleek Unicornfish	kala holo	51.1	Choat and Robertson (2002), Nadon, Kritzer (2001)
	NALI	*Naso lituratus*	Orangespine Unicornfish	umaumalei	25	Nadon, Kritzer (2001)
	NAUN	*Naso unicornis**	Bluespine Unicornfish	kala	33	Nadon et al. (2015) based on Eble (2009)
Carangidae	CAME	*Caranx melampygus**	Blue Trevally	‘omilu	47.5	Sudekum (1991), Nadon et al. (2015)
	CAOR	*Carangoides orthogrammus**	Island Jack	ulua	45.4	Nadon and Ault (2016)
	SECR	*Selar crumenophthalmus**	Big-Eyed Scad	akule	17	FishBase
	SEDU	*Seriola dumerili**	Amberjack	kahala	99.5	FishBase
Holocentridae	MYBE	*Myripristis berndti*	Bigscale Soldierfish	‘u‘u	17.5	Murty (2002), Nadon, Craig and Franklin (2008), Kritzer (2001)
Kyphosidae	KYSP	*Kyphosus species**	Lowfin Chub	nenue	25.3	Longnecker et al. 2012
Lethrinidae	MOGR	*Monotaxis grandoculis*	Bigeye Emperor	mu	38.9	Nadon and Ault (2016)
Lutjanidae	APVI	*Aprion virescens*	Green Jobfish	uku	50	Everson (1989), Nadon, O‘Malley
	LUFU	*Lutjanus fulvus*	Blacktail Snapper	to‘au	24	Nadon and Ault (2016)
	LUKA	*Lutjanus kasmira*	Bluestripe Snapper	ta‘ape	20	Allen (1985), Nadon, Loubens (1980), Kritzer (2001)
Mullidae	MUFL	*Mulloidichthys flavolineatus**	Yellowstripe Goatfish	weke	19.9	Cole (2009), Nadon, Estimated longevity
	MUVA	*Mulloidichthys vanicolensis**	Yellowfin Goatfish	weke ‘ula	20.6	Cole (2009), Nadon, Kritzer (2001)
	PACY	*Parupeneus cyclostomus*	Blue Goatfish	moano kea	26.9	Nadon and Ault (2016)
	PAPO	*Parupeneus porphyreus**	Whitesaddle Goatfish	kūmū	26.4	Nadon et al. (2015) that got from Moffitt (1979)
Scaridae	CACA	*Calotomus carolinus**	Stareye Parrotfish		24.3	DeMartini and Howard (2016)
	CHPE	*Chlorurus perspicillatus**	Spectacled Parrotfish	uhu uliuli	34.5	DeMartini and Howard (2016)
	CHSO	*Chlorurus sordidus**			17.2	DeMartini and Howard (2016)
	SCDU	*Scarus dubius**	Regal Parrotfish	lauia	23.2	Nadon and Ault (2016)
	SCPS	*Scarus psittacus**	Palenose Parrotfish	uhu	13.9	DeMartini and Howard (2016)
	SCRU	*Scarus rubroviolaceus**	Redlip Parrotfish	pālukaluka	35	DeMartini and Howard (2016)
Serranidae	CEAR	*Cephalopholis argus*	Blue-spotted Grouper		20	Schemmel et. al (2016)

* = Hā‘ena species list

Appendix 2. Hā‘ena resource fish species list and perceived conditions before the start of the 2016 surveys.

Listed Name	TaxonName	Hawaiian Name	Common Name	Family	Perceived condition
akule	*Selar crumenophthalmus*	*akule*	Big-Eyed Scad	Carangidae	Poor
moi	*Polydactylus sexfilis*	*moi*	Threadfin	Polynemidae	Poor
ama'ama	*Mugil cephalus*	*‘ama‘ama*	Striped Mullet	Mugilidae	Poor
kala	*Naso unicornis*	*kala*	Bluespine Unicornfish	Acanthuridae	Poor
nenue, Enenue	*Kyphosus species*	*nenue*	Chub	Kyphosidae	Excellent
	Kyphosus bigibbus	*nenue*	Brown Chub	Kyphosidae	Excellent
	Kyphosus cinerascens	*nenue*	Highfin Chub	Kyphosidae	Excellent
	Kyphosus vaigiensis	*nenue*	Lowfin Chub	Kyphosidae	Excellent
manini	*Acanthurus triostegus*	*manini*	Convict Tang	Acanthuridae	Good
oama	*Mulloidichthys flavolineatus*	*weke*	Yellowstripe Goatfish	Mullidae	Good
	Mulloidichthys vanicolensis	*weke ‘ula*	Yellowfin Goatfish	Mullidae	Good
āholehole	*Kuhlia sandvicensis*	*āholehole*	Hawaiian Flagtail	Kuhliidae	Fair
‘āweoweo	*Priacanthus meeki*	*‘āweoweo*	Hawaiian Bigeye	Priacanthidae	Fair
kahala	*Seriola dumerili*	*kahala*	Amberjack	Carangidae	Fair
ulua	*Carangoides ferdau*	*ulua*	Barred Jack	Carangidae	Fair
	Carangoides orthogrammus	*ulua*	Island Jack	Carangidae	Fair
	Caranx ignobilis	*ulua aukea*	Giant Trevally	Carangidae	Fair
	Caranx melampygus	*‘omilu*	Bluefin Trevally	Carangidae	Poor
	Caranx sexfasciatus	*ulua*	Bigeye Jack	Carangidae	Fair
	Gnathanodon speciosus	*ulua pa‘opa‘o*	Golden Trevally	Carangidae	Fair
	Pseudocaranx dentex	*ulua*	Thicklipped Jack	Carangidae	Fair
uhu	*Chlorurus spilurus*	*uhu*	Bullethead Parrotfish	Scaridae	Good
	Scarus psittacus	*uhu*	Palenose Parrotfish	Scaridae	Good
	Chlorurus perspicillatus	*uhu*	Spectacled Parrotfish	Scaridae	Good
	Calotomus carolinus	*uhu*	Star-eye Parrotfish	Scaridae	Good
	Calotomus zonarchus	*uhu*	Yellowbar Parrotfish	Scaridae	Good
	Scarus dubius	*lauia*	Regal Parrotfish	Scaridae	Good
	Scarus rubroviolaceus	*uhu*	Redlip parrotfish	Scaridae	Good
kūmū	*Parupeneus porphyreus*	*kūmū*	Whitesaddle Goatfish	Mullidae	
kawakawa	*Euthynnus affinis*	*kawakawa*	Wavy-back Tuna	Scombridae	Fair
palani	*Acanthurus dussumieri*	*palani*	Eye-stripe Surgeonfish	Acanthuridae	Good
maiko	*Acanthurus nigroris*	*maiko*	Bluelined Surgeonfish	Acanthuridae	Good

Appendix 3. The 29 resource fish species that were surveyed by year and by location in relation to the CBSFA boundaries. The number of individuals (n), the maximum size recorded (cm), and the average size and standard deviation by year and location (cm) are included. * Bolded "Species Name" are the species that were present in 13 or more transects (< 5%) out of the total 261.

Species Name*	Year	Location	n	Maximum Size (cm)	Mean Size (cm)	Standard Deviation
Acanthurus blochii	2016	HI	22	35	26	8.6
		HO	16	50	44	5.3
	2017	HI	207	40	30	8
		HO	37	35	28	9.4
	2018	HI	120	45	29	7.3
		HO	7	30	27	9.1
Acanthurus dussumieri	2016	HI	22	55	37	8.6
		HO	12	42	31	13.5
	2017	HI	21	45	32	5.5
		HO	15	45	37	6.9
	2018	HI	41	45	31	7.3
		HO	10	40	30	4.9
Acanthurus nigroris	2016	HI	17	24	16	5.9
		HO	28	22	16	3.7
	2017	HI	26	20	15	5.6
		HO	49	25	19	5
	2018	HI	25	24	15	5.1
		HO	12	18	18	1.7
Acanthurus triostegus	2016	HI	394	25	15	6
		HO	214	24	15	4.5
	2017	HI	640	25	16	2.6
		HO	245	20	17	2.2
	2018	HI	484	24	15	4.4
		HO	218	20	15	3.7
Aprion virescens	2016	HI	2	70	58	17.7
		HO	6	55	46	8.6
	2017	HI	5	80	57	21.3
		HO	6	100	66	21.6
	2018	HI	1	30	30	-
		HO	4	42	38	2.9
Calotomus carolinus	2016	HI	2	30	22	12
		HO	2	24	22	2.8
	2017	HI	20	34	15	10.6
		HO	9	43	28	8.8
	2018	HI	12	30	19	9.6
		HO	1	20	20	-
Carangoides orthogrammus	2016	HI	-	-	-	-
		HO	-	-	-	-
	2017	HI	1	15	15	-
		HO	-	-	-	-
	2018	HI	6	45	37	12.9
		HO	-	-	-	-

Caranx melampygus	2016	HI	40	55	26	9.1
		HO	3	35	25	9.1
	2017	HI	49	50	30	8.2
		HO	19	45	26	9.4
	2018	HI	90	45	30	6.3
		HO	9	35	28	4.2
Cephalopholis argus	2016	HI	15	50	32	9.6
		HO	4	32	24	6.3
	2017	HI	26	55	28	9.8
		HO	3	45	31	13.5
	2018	HI	16	50	32	9.3
		HO	6	40	36	6.6
Chlorurus perspicillatus	2016	HI	1	22	22	-
		HO	1	50	50	-
	2017	HI	9	50	25	13.9
		HO	3	54	51	2.3
	2018	HI	-	-	-	-
		HO	-	-	-	-
Chlorurus sordidus	2016	HI	223	36	16	5
		HO	-	-	-	-
	2017	HI	-	-	-	-
		HO	-	-	-	-
	2018	HI	-	-	-	-
		HO	-	-	-	-
Kyphosus species	2016	HI	27	31	27	3.3
		HO	137	35	25	3.2
	2017	HI	403	35	26	3.3
		HO	300	41	28	5.6
	2018	HI	242	45	26	6.1
		HO	336	36	21	3
Lutjanus fulvus	2016	HI	10	41	30	7
		HO	8	30	23	3.6
	2017	HI	17	28	23	3
		HO	3	28	26	1.7
	2018	HI	2	36	31	7.1
		HO	5	25	22	2.7
Lutjanus kasmira	2016	HI	46	27	21	2.8
		HO	89	32	29	3.4
	2017	HI	140	27	23	3.8
		HO	101	50	29	11
	2018	HI	78	30	18	4.5
		HO	418	25	21	1.7
Monotaxis grandoculis	2016	HI	45	40	24	7.1
		HO	31	30	23	4.4
	2017	HI	42	35	26	7.4
		HO	45	40	28	4.8
	2018	HI	26	40	32	7.5
		HO	82	30	29	5
Mulloidichthys flavolineatus	2016	HI	12	24	23	0.4
		HO	-	-	-	-
	2017	HI	73	30	23	7.5
		HO	200	13	13	0
	2018	HI	35	35	22	4.6
		HO	2	18	18	0

Mulloidichthys vanicolensis	2016	HI	15	14	14	0
		HO	42	26	25	0.7
	2017	HI	164	31	25	4.9
		HO	350	30	24	7.3
	2018	HI	110	30	16	4.2
		HO	49	30	22	3.7
Myripristis berndti	2016	HI	37	25	24	0.5
		HO	16	30	22	4.3
	2017	HI	7	25	23	3.4
		HO	101	25	17	2.2
	2018	HI	12	34	21	6.2
		HO	15	18	18	0
Naso brevirostris	2016	HI	20	15	15	0
		HO	-	-	-	-
	2017	HI	-	-	-	-
		HO	1	33	33	-
	2018	HI	-	-	-	-
		HO	-	-	-	-
Naso hexacanthus	2016	HI	1	20	20	-
		HO	62	22	20	2.7
	2017	HI	17	25	22	4.3
		HO	35	36	26	2.6
	2018	HI	33	30	22	6.9
		HO	-	-	-	-
Naso lituratus	2016	HI	80	42	24	5.9
		HO	39	40	28	7.3
	2017	HI	125	35	26	5.2
		HO	93	45	28	5.5
	2018	HI	112	40	25	5.7
		HO	44	35	26	2.9
Naso unicornis	2016	HI	74	50	28	7.2
		HO	38	50	31	9
	2017	HI	104	60	30	7.8
		HO	100	55	34	7.7
	2018	HI	112	40	24	7.3
		HO	10	50	36	12.2
Parupeneus cyclostomus	2016	HI	9	50	34	12.3
		HO	4	40	26	14.2
	2017	HI	22	45	28	10.9
		HO	12	42	21	11.7
	2018	HI	24	33	18	10.5
		HO	14	35	8	7.9
Parupeneus porphyreus	2016	HI	-	-	-	-
		HO	1	30	30	-
	2017	HI	2	28	28	0
		HO	-	-	-	-
	2018	HI	2	35	30	7.1
		HO	-	-	-	-
Scarus dubius	2016	HI	-	-	-	-
		HO	-	-	-	-
	2017	HI	4	26	25	1.7
		HO	-	-	-	-
	2018	HI	-	-	-	-
		HO	-	-	-	-

Scarus psittacus	2016	HI	26	22	20	2
		HO	-	-	-	-
	2017	HI	38	30	20	6.5
		HO	6	7	6	0.5
	2018	HI	10	30	23	6.3
		HO	4	18	17	1.2
Scarus rubroviolaceus	2016	HI	160	70	26	22.1
		HO	54	55	37	9.8
	2017	HI	242	70	42	14.5
		HO	124	65	41	10.4
	2018	HI	184	65	44	13.5
		HO	22	65	55	12.4
Selar crumenophthalmus	2016	HI	-	-	-	-
		HO	-	-	-	-
	2017	HI	-	-	-	-
		HO	-	-	-	-
	2018	HI	4	20	20	0
		HO	-	-	-	-
Seriola dumerili	2016	HI	-	-	-	-
		HO	-	-	-	-
	2017	HI	4	48	44	4.6
		HO	2	41	41	0
	2018	HI	2	50	50	0
		HO	6	65	50	11.8

Appendix 4. Displaying only significant ($p \leq 0.05$) Tukey pairwise comparisons from the generalized linear model (GLM). Note: Inside (HI), outside (HO), aggregate reef (AGRE), and pavement (PAVE). Reference Appendix 1 for species code definitions.

Combination 1			Combination 2			Estimate	Standard Error	Z ratio	P Value
HI	AGRE	ACBL	HI	PAVE	ACBL	0.03	0.004	6.1	0.000020
HI	AGRE	ACBL	HO	PAVE	ACBL	0.04	0.006	6.4	0.000002
HO	AGRE	ACBL	HO	PAVE	ACBL	0.03	0.004	6.1	0.000020
HI	AGRE	ACDU	HI	PAVE	ACDU	0.03	0.004	6.1	0.000020
HI	AGRE	ACDU	HO	PAVE	ACDU	0.04	0.006	6.4	0.000002
HO	AGRE	ACDU	HO	PAVE	ACDU	0.03	0.004	6.1	0.000020
HI	AGRE	ACNR	HI	PAVE	ACNR	0.03	0.004	6.1	0.000020
HI	AGRE	ACNR	HO	PAVE	ACNR	0.04	0.006	6.4	0.000002
HO	AGRE	ACNR	HO	PAVE	ACNR	0.03	0.004	6.1	0.000020
HI	AGRE	ACTR	HI	PAVE	ACTR	0.03	0.004	6.1	0.000020
HI	AGRE	ACTR	HO	PAVE	ACTR	0.04	0.006	6.4	0.000002
HO	AGRE	ACTR	HO	PAVE	ACTR	0.03	0.004	6.1	0.000020
HI	AGRE	APVI	HI	PAVE	APVI	0.03	0.004	6.1	0.000020
HI	AGRE	APVI	HO	PAVE	APVI	0.04	0.006	6.4	0.000002
HO	AGRE	APVI	HO	PAVE	APVI	0.03	0.004	6.1	0.000020
HI	AGRE	CACA	HI	PAVE	CACA	0.03	0.004	6.1	0.000020
HI	AGRE	CACA	HO	PAVE	CACA	0.04	0.006	6.4	0.000002
HO	AGRE	CACA	HO	PAVE	CACA	0.03	0.004	6.1	0.000020
HI	AGRE	CAME	HI	PAVE	CAME	0.03	0.004	6.1	0.000020
HI	AGRE	CAME	HO	PAVE	CAME	0.04	0.006	6.4	0.000002
HO	AGRE	CAME	HO	PAVE	CAME	0.03	0.004	6.1	0.000020
HI	AGRE	CEAR	HI	PAVE	CEAR	0.03	0.004	6.1	0.000020
HI	AGRE	CEAR	HO	PAVE	CEAR	0.04	0.006	6.4	0.000002
HO	AGRE	CEAR	HO	PAVE	CEAR	0.03	0.004	6.1	0.000020
HI	AGRE	KYSP	HI	PAVE	KYSP	0.03	0.004	6.1	0.000020
HI	AGRE	KYSP	HO	PAVE	KYSP	0.04	0.006	6.4	0.000002
HO	AGRE	KYSP	HO	PAVE	KYSP	0.03	0.004	6.1	0.000020
HI	AGRE	LUFU	HI	PAVE	LUFU	0.03	0.004	6.1	0.000020
HI	AGRE	LUFU	HO	PAVE	LUFU	0.04	0.006	6.4	0.000002
HO	AGRE	LUFU	HO	PAVE	LUFU	0.03	0.004	6.1	0.000020
HI	AGRE	LUKA	HI	PAVE	LUKA	0.03	0.004	6.1	0.000020
HI	AGRE	LUKA	HO	PAVE	LUKA	0.04	0.006	6.4	0.000002
HO	AGRE	LUKA	HO	PAVE	LUKA	0.03	0.004	6.1	0.000020
HI	AGRE	MOGR	HI	PAVE	MOGR	0.03	0.004	6.1	0.000020
HI	AGRE	MOGR	HO	PAVE	MOGR	0.04	0.006	6.4	0.000002
HO	AGRE	MOGR	HO	PAVE	MOGR	0.03	0.004	6.1	0.000020
HI	AGRE	MUFL	HI	PAVE	MUFL	0.03	0.004	6.1	0.000020
HI	AGRE	MUFL	HO	PAVE	MUFL	0.04	0.006	6.4	0.000002
HO	AGRE	MUFL	HO	PAVE	MUFL	0.03	0.004	6.1	0.000020
HI	AGRE	MUVA	HI	PAVE	MUVA	0.03	0.004	6.1	0.000020
HI	AGRE	MUVA	HO	PAVE	MUVA	0.04	0.006	6.4	0.000002
HO	AGRE	MUVA	HO	PAVE	MUVA	0.03	0.004	6.1	0.000020
HI	AGRE	NALI	HI	PAVE	NALI	0.03	0.004	6.1	0.000020
HI	AGRE	NALI	HO	PAVE	NALI	0.04	0.006	6.4	0.000002
HO	AGRE	NALI	HO	PAVE	NALI	0.03	0.004	6.1	0.000020
HI	AGRE	NAUN	HI	PAVE	NAUN	0.03	0.004	6.1	0.000020
HI	AGRE	NAUN	HO	PAVE	NAUN	0.04	0.006	6.4	0.000002
HO	AGRE	NAUN	HO	PAVE	NAUN	0.03	0.004	6.1	0.000020
HI	AGRE	PACY	HI	PAVE	PACY	0.03	0.004	6.1	0.000020
HI	AGRE	PACY	HO	PAVE	PACY	0.04	0.006	6.4	0.000002
HO	AGRE	PACY	HO	PAVE	PACY	0.03	0.004	6.1	0.000020
HI	AGRE	SCPS	HI	PAVE	SCPS	0.03	0.004	6.1	0.000020
HI	AGRE	SCPS	HO	PAVE	SCPS	0.04	0.006	6.4	0.000002
HO	AGRE	SCPS	HO	PAVE	SCPS	0.03	0.004	6.1	0.000020
HI	AGRE	SCRU	HI	PAVE	SCRU	0.03	0.004	6.1	0.000020
HI	AGRE	SCRU	HO	PAVE	SCRU	0.04	0.006	6.4	0.000002
HO	AGRE	SCRU	HO	PAVE	SCRU	0.03	0.004	6.1	0.000020